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SPECIES-BUILDING BY HYBRIDIZATION AND MUTATION

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THE mystery that has surrounded the origin of new species in the incipient stages of their evolution has lately been penetrated and cleared away to a large extent by the light of studies in Mendelian inheritance and the attendant idea of mutation. Species building is no longer a hypothetical process based on the preservation of minute, useful, fortuitous variations, but it is a process open to observation and experimental control. Its raw materials are variations that are usually not minute, useful or fortuitous, but clean-cut unit characters, tending to vary only in certain limited, well-defined directions depending upon the chemical peculiarities and physical structure of the particular form of protoplasm, and, in the vast plurality of cases, nonuseful.

The fields of systematic zoology and botany, illuminated by the new science, genetics, are emerging from the mists of formalism, and invite biologists of the broadest type to exploration. The geneticist turns to systematics for many of the materials with which to solve the problems of organic evolution. The systematist sees that in order to keep abreast of the times he must stand ready to rebuild his pigeonholes and test with experiment that which he puts into them.

Every one occupied with zoology or botany realizes that there are no adequate criteria by which this or that assemblage of individuals is or is not to be regarded as a

distinct species. Arbitrary rules for species making, designed to restrict the activities of the more vigorous "splitters" have been indeed laid down by experienced and conservative systematists. The final test, however, so far as any exists, is acknowledged to be whether a group breeds approximately true to its kind and is approximately sterile with other closely related stock, and yet in how few cases have both or either of these criteria been actually applied by the describer of species!

As a matter of fact no stock that has been bred on a vast scale, so far as I am aware, breeds absolutely true to specific characters. In Morgan's *Drosophila*¹ and De Vries's *Enothera*, numerous mutants appear, probably through the absence of certain chemical elements, or by unusual combinations of elements, in the chromatin of the germ plasm. That this phenomenon has not been shown for many other species is due, in all probability, to lack of close attention to all the individuals in a huge procession of stock in the process of breeding. Any insect bred as extensively as *Drosophila ampelophila*, the pomace fly, has been would probably show as many mutants; some would show more. *Colias eurytheme*, the "orange sulphur" or alfalfa butterfly, is such an example. Though this butterfly can not be bred on a scale comparable with *Drosophila*, every thousand individuals yield many discontinuous variations: red eyes instead of green, tongue uncoiled instead of wound in close flat spiral when at rest, one antenna shorter than the other, the absence of certain spots from the wings, gynandromorphism, caterpillars with two longitudinal rows of large black dorso-lateral spots or white dorso-lateral stripes upon a dorsal surface usually unmarked, caterpillars with one proleg less upon one side than the other. This is a partial list of points at which the descendants of three females of *Colias eurytheme* failed in a single summer to breed true to the characteristics of the species, though bred under uniform normal conditions. The fact that these discontinuous

¹ *Science*, N. S., Vol. XXXIII, Nos. 847, 849, pp. 496-499, 534-537, 1911.

variations appear under uniform external conditions leads one to be very skeptical toward most of the past experimental work supposed to show the effects of the environment upon insects in modifying the germ cells. Any one wishing to try an experiment on the production of variations by the influence of the environment, or upon the inheritance of acquired characteristics, should deny himself absolutely this privilege until he shall have bred under normal conditions at least a thousand individuals of the stock that he will subsequently employ.

That species necessarily breed true to the specific characters ascribed to them by their inventors is an unverified dogma. At best the reporter picks out stray individuals here and there from a vast procession of which he can only see glimpses, and, trusting to the credulity of the public in the established ideas about these matters, he creates upon paper a new species. Doubtless the unit characters of "specific" grade in the stock of some species are more generally constant or homozygous than those of certain others, but it is reasonable to suppose that, owing to dominance the heterozygous² condition regarding certain characters is frequently masked and unnoticed in apparently pure strains of wild stock. If the heterozygote respecting a certain character be comparatively rare, or if it be a heterozygote based on several interacting factors, like redness in the kernel of Nilsson-Ehle's wheat,³ it may cross again and again with the homozygous dominant, or with another heterozygote of similar nature to itself, without the appearance in the population of the recessive. That specific and varietal characters do exist in heterozygous condition in wild stock of "pure" species, unmasked by dominance and easily detected, I have found to be the case in *Colias* at several points. The color pattern as a whole apparently fluctuates in variation, but these variations in detail are

² The mixed Mendelian condition, $D(R)$, producing germ cells D and R in equal numbers.

³ *Act. Univers. Lund*, 1909.

strictly a matter of inheritance. Its "fluctuation" is not due to a difference in environmental conditions surrounding different individuals, but evidently to the condition of the germ plasm. The parents of any brood may be heterozygous or homozygous for the determiners of color pattern. If they come from a strain homozygous in this respect and are alike in appearance, the offspring will resemble the parents closely and show a narrow range of variation, but if unlike and derived each from unlike parents, a wide range of inherited "fluctuation" occurs. Such is often the case in the inheritance of a melanic tendency so often attributed to the action of the environment, and of spots used in the diagnosis of species as, for example, the conspicuous spot in the middle of the under side of the hind wing. This is commonly double in *Colias philodice* and *C. eurytheme*, consisting of a chief and an accessory spot, single in *C. paleno*, an arctic circumpolar species, but it varies enormously. In *eurytheme* and *philodice* the accessory spot may be absent; in *paleno*, in rare cases, it may be present. I have bred large families of *C. eurytheme* in which both the chief and accessory spots were, like those of the parents, almost uniformly large and nearly equal in size. In other families, from parents in which the accessory spot is nearly or quite lacking, the offspring show a similar reduction. In *C. philodice* I have found it possible by selection to establish a race devoid of the row of submarginal red-brown spots of the under side of the wings. Thus, by selection, strains, nearly or perhaps quite homozygous for definite points of color pattern, may be established, derived from a population which in the main is in an extremely heterozygous condition. Yet species are named and distinguished on the basis of these features.

Another example of heterozygous condition of a character within a wild species is the white pigment in the ground color of the "albino" female of *Colias*, both in the yellow species, *philodice* and the orange species, *eurytheme*. The white female is regularly heterozygous

for this sex-limited character. Her daughters are white or colored (yellow or orange, as the case may be) in equal numbers. Still another interesting heterozygous feature, though not of "specific" grade, was seen last summer in a pure strain of *Colias eurytheme*. A female appeared that could not upon stimulation coil up her tongue. Mated with a normal male, this abnormality was inherited in various degrees by half her offspring (37 uncoiled and 28 coiled). One of her daughters, abnormal in this respect and mated with a normal of a different strain, transmitted the abnormality to about 16 per cent. of her offspring (29:151), showing that the possessor of this abnormality is regularly heterozygous in respect to it.

Whether *Ænothera lamarckiana* is or is not a complex hybrid produced from two American species, is it not certain that, like other wild and cultivated stock, it does possess characters for which it is heterozygous, and that the watcher for mutants frequently seizes upon rare combinations of recessive features as a part of his elementary species?

But to breed true is only a secondary criterion of species. Inbred strains of domestic animals and plants do that to a certain degree. Varieties and races to a certain extent may do the same. The real criterion (and the one least often practically used by the systematist) is fertility within the group and sterility with other closely related groups. Here dogma holds sway among writers on organic evolution as well as among systematists, for we are told by those who have been accustomed since childhood to the idea of the objective reality of species that hybridization of species, that is, genuine species in good and regular standing before the scientific public, has played very little part in the origin of new species. This attitude was entirely logical in view of the accepted ultimate definition of a species. If the individuals of one species are actually sterile with members of another, hybridiza-

tion of species can not play an important part in the manufacture of new wild strains. But only in comparatively rare instances have attempts been made experimentally to mate Linnæan species. The dogma of the objective reality and uniform value of the species unit has diverted us from seriously attacking this problem. Just as in the nineteenth century the fixed idea of the immutability of species blocked the progress of the doctrine of evolution, so this dogma now stands in our way, and obstructs the possibility of vision. We need now fully to recognize the fact, which most biologists are ready to admit, that the term species is applied to most heterogeneous groups of individuals, groups of every conceivable size, based on differences that are most diverse in number and importance, often separated from allied groups entirely by the arbitrary judgment of the describer, and depending ultimately upon his personal temperament. These groups, as already stated, have been tested in comparatively few instances by the only reputable criterion that can be applied in the separation of closely allied groups, that of sterility or fertility *inter se*.

To one who tries to divest himself of the accepted ideas regarding species and is on the watch for evidence of hybridization among unlike strains that we are accustomed to call species, new cases of such hybridization frequently come to light. Especially is this true among the insects. In regions where the faunal areas of two "good" species overlap or are contiguous, such crossing not infrequently occurs.

A most interesting case is that of the four species of the coccinellid beetle *Adalia* that occur in the same region in Colorado, as worked out by Palmer.⁴ These four forms with clean-cut differences in color and color pattern had been named and described by different authors as distinct species, yet three of them were found to be interbreeding with complete fertility but still respectively maintaining their identity, forming a regular Mendelian

⁴ *Annals Entom. Soc. America*, IV, 3, September, 1911.

epistatic series: a red-brown spotless form, *melanopleura*, dominant at one end of the series, then *annectans*, a red-brown, spotted type, and finally the recessive, melanic, red-spotted *humeralis* with a color pattern different from that of *annectans* or of *Coloradensis*, another red-brown, spotted type of that locality. "But" says the upholder of the present idea of species, "here we have a single polymorphic species, not three or four different species. The breeding experiments show that the describers of these forms were wrong in ascribing systematic rank to mere color varieties." It goes, of course, almost without saying that the makers of these species did not before naming their beetles, breed them to determine whether they would breed true to type and were infertile *inter se*. Indeed, in how few cases has this been done! Even the larval stages of most known beetles are imperfectly unknown, much less the possible genetic relationship of one type to another, as determined by breeding them to maturity. Blaisdell⁵ describes the case of two Californian Coccinellidæ which are found in winter in small groups under the bark of eucalyptus trees. "Usually there was one *Olla plagiata* with each of the groups [of *O. abdominalis*], irrespective of whether they were made up of two or more individuals." The same author, by selection of specimens of *abdominalis* representing different types of color pattern, describes its range of variation, but adds that his studies throw no light on the relationship of the two species. Had he bred certain individuals of *O. abdominalis* together, it is not at all unlikely, in view of his observation of the regular occurrence of a few *plagiata* in every group of *abdominalis*, that the former interbreeds with the latter and may be a simple recessive in respect to it. Miss Palmer's work on the allied *Adalia* certainly suggests this as a possibility.

Another remarkable case is that of the nine true-breeding species of grouse-locust, *Paratettix*, recently de-

⁵ *Entom. News*, Vol. 24, No. 9, November, 1913.

scribed by Nabours.⁶ These nine color types, or species, freely interbreed. The color pattern of the resulting F_1 hybrid in each case is a mosaic combination of those of the two parents. The latter in subsequent inbreeding may be extracted intact, each having been transmitted as a distinct unit, without dominance.

In Lepidoptera, an order in which polymorphism is notoriously common, hybridization between species has been frequently observed. Standfuss⁷ devotes eight octavo pages of his excellent "Handbuch" simply to the enumeration of examples of such hybridization between palæarctic species of moths and butterflies, and acknowledges that he mentions only a fragment of all such cases on record or preserved in collections. This list would be greatly extended if American species were included. Seven different hybrid combinations within the genus *Colias* in the palæarctic region have been noted by Standfuss.

Colias philodice, the clouded sulphur or clover butterfly of the eastern and central United States, readily crosses with *C. eurytheme*, the orange sulphur or alfalfa butterfly of the western and central states. The territory of *philodice*, according to Scudder extends like a wedge westward from the Atlantic into the faunal area of *eurytheme*. Overlapping thus occurs in the Mississippi Valley, though *philodice* does not extend as far southward as the Gulf States, Texas, Louisiana and Mississippi, in which *eurytheme* is found.

These two species are fairly sharply distinguished by the difference in the ground color, which in *eurytheme* is orange, in *philodice* sulphur yellow. The middle spot of the upper side of the hind wing is brilliant orange in *eurytheme*, pale orange or yellow in *philodice*. The dark border of the hind wing of the female is wider in *eurytheme* than in *philodice* and broken with a row of large yellow spots.

⁶ *Journal of Genetics*, Vol. 3, No. 3, February, 1914.

⁷ "Handbuch d. paläarktischen Gross-Schmetterlinge," 1896, p. 51-53.

It has long been known that these two species hybridize in the Mississippi Valley, where both occur. By extended experiments during the past summer and previous autumn with *eurytheme* stock sent to me from Arizona through the kindness of Messrs. V. L. Wildermuth and R. N. Wilson and with *philodice* from New Hampshire, I have found that the two species mate together readily, and produce vigorous offspring. The species-hybrid males were then mated with *eurytheme* females, and more than half of the pairs (viz., four out of seven) were fertile. Mated together, however, the species-hybrids showed much sterility. Out of ten such matings, nine were infertile. From the tenth pair, nineteen adult butterflies were produced.

Orange in this cross is distinctly dominant over no orange, or yellow, but the color of the heterozygote is a pale orange overlying yellow, and is by no means as brilliant as the almost fiery orange of the large, summer seasonal variety, the typical "*eurytheme*." In broods emerging the last week in August and the first three weeks of September, when intense color may be expected, the heterozygote is pale orange, corresponding approximately to the variety known as *keewadin*, whereas those raised in the greenhouse and emerging early in December, resemble the small orange-yellow winter type known as *ariadne*. *Keewaydin*, according to Wright,^s occurs at all seasons in California, though probably more abundantly in spring and autumn. Hence he regards this as the typical variety, rather than "*eurytheme*." It is intermediate, however, in size and intensity of color.

In general, therefore, there is an incomplete dominance of orange, the color of the heterozygote corresponding either to that of the intermediate or to that of the winter, seasonal variety of *eurytheme*, depending upon the time of the year when, and the environmental condition under which, the cross is made. The wide, spotted margin of the hind wing in the female *eurytheme*, moreover, when pres-

^s "Butterflies of the West Coast of the United States," p. 119.

ent in marked degree, is dominant over the narrower margin in *philodice*. This dominance of the orange manifests itself quite as distinctly if the albino female of *eurytheme*, instead of the orange female, is bred to the yellow *philodice* male. The daughters of such a family in one case (0, 1913) were 36 white, 35 orange; the sons, numbering 72, were, of course, all orange. The white species-hybrid (F_1) is identical in appearance with the albino *eurytheme*, the female color pattern of the latter (wide marginal bands) being dominant, and the orange middle spot both in pure bred albino *eurytheme* and in the albino hybrid being usually paler than in their orange sisters.

The second hybrid generation inbred (F_2) shows a well marked segregation of the sulphur-yellow color of *philodice*, as a simple Mendelian recessive. Three out of the sixteen colored (non-albino) individuals of the brood obtained in December, 1913, are definite recessives of clear sulphur yellow, with pale yellow middle spots on the hind wing. The most highly colored individuals are four that correspond in hue to pale examples of the light orange-yellow winter variety, *ariadne*. There is no return, at least in this winter brood (enclosed in a greenhouse in New Hampshire in December), to the brilliant orange of the grandparental *eurytheme* stock. Nor do they even return to the suffused light orange (intermediate) tint of the heterozygous father (*keewadin* type), for the ground color of all individuals of this brood (F_2) is yellow, either flushed or spotted, except in three individuals, with orange.

An interesting case of probable hybridization in the allied genus *Meganostoma*, or dog's head butterfly, is recorded by Wright⁹ between the Californian *M. eurydice* and *M. casonia*, common throughout the southern states. The two species are remarkably different in color and have different food plants. The male of *eurydice* differs from that of *casonia* in having a violet luster and lacking

⁹ Loc. cit., p. 116.

the black border upon the hind wings possessed by *cæsonia*; in the female, *eurydice* is clear yellow with no dark border, while in *cæsonia* the female has a wide border similar to that of its male, though less well marked on the hind wings. The probable hybrid called *amorphæ* is a female, intermediate in color between the typical *cæsonia* and *eurydice*. That is, the border of *cæsonia* crossed with no border (if my interpretation is correct) is incompletely dominant. Wright says:

At one time I was of the opinion that *Amorphæ* was a hybrid between *Eurytheme* and *Caesonia* . . . but of late years, as no male *Amorphæ* is known, I have concluded that *Amorphæ* is simply a dimorphic female [of *eurydice*].

Possibly it is both, an example of dimorphism produced either by immediate hybridization, or by a mutation resulting from some previous hybridization. That a male appears to be lacking in this case would not be an argument against the possibility of hybridization, for by such crossing the sex ratio is frequently upset, the product being of one sex only. But it appears to be possible that the male of this cross is that described as *M. bernardino*, a variety of *eurydice* found in the mountains of the same region where *amorphæ* also occurs. It is an interesting combination of the male coloration of both species, having the violet hue of *eurydice* that is lacking in *cæsonia* and having the dark border of the hind wings of *cæsonia* lacking in *eurydice*. Its female is described as being smaller than that of *eurydice*, but otherwise practically identical with it. This case, as Wright has suggested, is a most inviting subject for further study, and, judging by what he says of the sexual instincts of the *eurydice* male—"a wooer . . . energetic and persistent, not hesitating to ignore all rules of propriety, of species and of genera"—not difficult of experimental management.

The genus *Basilarchia*, the admiral butterflies, is well known for the hybridization of its very unlike species, *B. arthemis* the "banded purple" of the northern states,

B. astyanax the "red-spotted purple" of the southeastern states. The hybrid species, *B. proserpina*, occurs in a zone in which their two faunal areas overlap. In this same group is the common "viceroy" *B. archippus*, the range of which roughly covers that of both the other species and extends further westward, touching the Pacific coast in Washington (Scudder). The experiments of Edwards, and especially of Field, have shown that these three well-differentiated pure species occupying contiguous, or in respect to *archippus* overlapping, territory are in some cases at least mutually fertile. *B. arthemis* and *astyanax* regularly interbreed in the narrow zone where *proserpina* occurs. *Proserpina*, the hybrid, usually shows the general dominance of the *astyanax* characters (lack of white band).

From eggs laid by a wild female *proserpina* Edwards¹⁰ secured three *arthemis*, one *proserpina*. Field¹¹ raised from a similar lot of eggs nine *proserpina*, seven *arthemis*. Presumably in each case the male parent was the recessive *arthemis*, and hence equal numbers of the two types would be expected. Field has also succeeded in crossing a ♀ *astyanax* with a ♂ *arthemis*, and a ♀ viceroy, *archippus*, with a ♂ *arthemis*, the latter pair producing nine males intermediate in color. Specimens of an apparent hybrid, intermediate in color between *astyanax* and *archippus*, have also occasionally been captured.

The complete overlapping of the faunal area of *archippus* upon those of the two other species indicates that, though crossing sometimes occurs, the resulting hybrids are probably usually sterile, though this matter has not yet been thoroughly investigated. *Proserpina*, however, is a fertile and extraordinarily variable hybrid. In view of its great variability it appears, by the way, not impossible that *archippus*, the red-brown "mimic" of the monarch, *Anosia plexippus*, may have arisen as a mutation from the hybrid *proserpina*, though the wide-spread

¹⁰ *Canadian Entomologist*, Vol. IX, 1877.

¹¹ *Psyche*, Vol. XVII, No. 3, 1910.

range of *archippus* at present and our ignorance of the state of the *Basilarchia* stock at the time of the origin of the "mimic" make any such specific historical guess hazardous. It may, however, some time be possible by experimental breeding to extract from this red-spotted purple hybrid a red-brown type similar to *archippus*. If the *Basilarchia* stock were as easily bred as *Drosophila*, one might be very confident of accomplishing this. In any event, the theory of the origin of mimicry by natural selection is, in the opinion of the writer, entirely superfluous, though this celebrated monarch-vice-roy case should be exhaustively studied by experimental methods, to determine whether natural selection now operates in any degree in the matter.

Examples of clusters of interbreeding types may be drawn in large numbers from various classes of animals and plants. Bateson¹² has recently called attention to the interesting case of the two American flickers described by Allen,¹³ the eastern *Colaptes auratus* and the western and Mexican *C. cafer*, which hybridize in the zone in which their faunal areas overlap, the American grackles, the golden-winged and blue-winged warblers and their hybrids, Lawrence's and Brewster's warblers, and others.

In reference to the common purple grackle, which Chapman¹⁴ regards as a hybrid between the Florida grackle and the bronzed grackle, Ridgeway¹⁵ says:

My own opinion in the matter exactly coincides with Mr. Chapman's but since so many forms now ranked as sub-species are similarly involved I prefer, at present, to leave the matter in abeyance.

This significant statement from a master of ornithological taxonomy indicates that hybridization among American birds is a promising subject for investigation.

Of the occasional mutual fertility of unlike strains different enough to be classed as unquestionable species,

¹² "Problems of Genetics," 1913, Chap. VII.

¹³ *Bull. American Mus. Nat. Hist.*, Vol. IV, 1892.

¹⁴ *Ibid.*

¹⁵ "Birds of North and Middle America," Part 2, p. 219, 1902.

there also can be no doubt. "We can only escape the conclusion that some species are fully fertile when crossed," wrote Darwin,¹⁶ "by determining to designate as varieties all the forms that are quite fertile," and he added that some plants exposed to unnatural conditions are so modified "that they are much more fertile when crossed by a distinct species than when fertilized by their own pollen."

The rareness of these crosses between unlike strains or species and the partial sterility of the offspring are not obstacles in the way of regarding occasional hybridization as one of the chief sources of mutation and hence eventually of new species, for, as my preliminary experiments in hybridizing species of *Colias* have already shown, there may exist within a strain of species-hybrids certain individuals that are fertile, though the most of their brothers and sisters, mated, respectively, in a similar way, are sterile. Nature probably makes more random experiments in hybridization than we imagine; many fail; some succeed; and in especially favorable stock like *Colias*, judging from the numbers of closely allied but different types (species) occurring in the same localities in western Asia or in northwestern United States and British America, probably many succeed.

In seeking to determine how mutation, whether the result of hybridization or of possible climatic influences, acts in the production of new species, it is possible from cases already at hand to suggest possible steps in the evolution of distinct, mutually infertile, types from one comparatively simple polymorphic species.

The well-known dimorphic European currant moth, *Abraxas grossulariata*, in which the light-colored (recessive) variety, *lacticolor*, is found in nature only in the female sex, will serve as an example of an elementary condition. *Lacticolor* males, as Doncaster¹⁷ has shown,

¹⁶ "Animals and Plants under Domestication," Vol. II, Chap. 19, p. 179.

¹⁷ "Report of the Evolution Committee," 4, 1908.

may readily be bred. When one of these males is mated with a *lacticolor* female, there is produced in captivity a pure *lacticolor* strain. If *lacticolor* males and females should be segregated and allowed to breed together until they have become as abundant as the typical form, this case would then resemble that of the Colorado lady beetles of the genus *Adalia*, described above, in that it would consist of different types maintaining their identity while freely interbreeding with complete fertility. The *Abraxas* complex differs from the *Adalia* species-cluster, however, in the occurrence of sex-linkage in the inheritance of the *lacticolor* variety, whereas in *Adalia* the factors for the different color patterns apparently are distributed in the gametogenesis of a heterozygous individual without sex-linkage, freely and at random.

A more advanced stage in evolution is that represented by the *Basilarchia* species-cluster, in which partial sterility between the viceroy and the two purple species, over the faunal areas of which its own overlaps, and the difference in geographical distribution between the banded purple and red-spotted purple, keep the three elements apart.

By easy stages we may in imagination pass on to groups composed of closely allied species which sterility and local segregation completely separate from one another, groups that probably have arisen from a polymorphic species that has broken up into its constituent parts, and thus given rise to new elementary species.

The dimorphism of *Colias* differs from that of *Abraxas* in that the color of the rarer type of female can not be transferred in the ordinary course of breeding, without further mutation, to the male. It is a sex-limited character, like the female color pattern in *Colias*, (*i. e.*, a wide dark border broken with spots) and not sex-linked like the variety *lacticolor* of *Abraxas*.

The white female of *Colias* is regularly heterozygous for color. She produces as many white daughters as

yellow, or orange, as the case may be. Evidently, in order to extract a pure white race from *C. philodice* or *C. eurytheme*, it will be necessary by a mutation to obtain first a homozygous white female, and then by a further mutation a homozygous white male. White males are known in nature as rare aberrations, but, whether they are homozygous or heterozygous for color, it is impossible to say. Among the two thousand offspring of heterozygous white females of *philodice* and *eurytheme* that I have bred since 1908, there has been not a single white male. The sons of a white female, though some are capable of transmitting the white, are always yellow or orange. I have lately, however, raised a large brood in which all the females were white. This was a "back cross" between a white female of the orange *eurytheme* and a male species-hybrid (son of a white mother). Precisely similar matings, however, gave both white and colored female offspring in equal numbers; hence in the production of this brood there was probably a mutation. From such stock as this the extraction of a pure white race from *Colias* at some time may possibly be accomplished.

In this connection it is interesting to note that we have the testimony of a good observer, the late Mr. W. G. Wright,¹⁷ who made the study of Californian butterflies his life work, to the effect that the white variety of *Colias eurytheme* "is now quite common, though twenty-five years ago it was a great rarity, and it was accounted a feat to secure one of them, and if the present rate of increase of the blond form shall go on, in a few hundred years the normal orange-colored female will be extinct and unknown." If this is a fact, and not an illusion due to a general increase in the population of *eurytheme* owing to an increase in the cultivation of the food plant, alfalfa, in that region, it may be the result of possible mutations, whereby homozygous white females may have been introduced into the population. It will be of inter-

¹⁷ *Loc. cit.*, p. 117.

est to determine whether such true-breeding white females actually occur in California.

Evolution in *Colias* is usually regarded, on the other hand, as tending towards suppression of the white stock rather than its further extension, inasmuch as *Pieris* and other allied genera are white. It seems to be a reasonable hypothesis that, by progressive mutations in *Colias* affecting first the male then the female,¹⁸ white has become yellow; yellow, orange; orange, red, or a fiery orange;¹⁹ or yellow may be transmuted into black, as in an aberration of the male in *C. philodice*. By retrogressive or degressive mutations, accordingly, we may hope to isolate from *C. philodice* or *C. eurytheme* a pure white race.

SUMMARY AND CONCLUSIONS

The erroneous idea that Linnæan species are homogeneous, well-defined groups of equal importance has done much to retard progress in the experimental study of evolution. The limits of a species are often arbitrary, depending ultimately upon the temperament of the describer, and frequently based upon ignorance of the nearest allies of the individuals described, living in other parts of the world.

The most definite criteria of species, viz., that "specific" characters are constant, and that hybrids of Linnæan species are infertile *inter se*, are only approximately correct. Characteristics of species sometimes occur in heterozygous condition. Hybrids of Linnæan species, as has long been known, are often fertile. These matters, owing to traditional, unwarranted respect for described species, have received comparatively little investigation.

Examples of hybridization in *Adalia*, *Colias*, *Meganotoma*, *Basilarchia* and *Paratettix* among insects, in *Colaptes*, *Quiscalus*, and *Helminthophila* among birds are cited.

¹⁸ In *C. dimera* of South America, for example, the female is yellow, but in the male the fore wings are orange.

¹⁹ As in the Asiatic *eogene*.

Occasional fertile crossing of unlike strains that rarely interbreed is a probable source of mutations and new types.

A suggestion is made that a comparatively simple polymorphic species (like *Abraxas grossulariata*) may break up into a cluster of mutually fertile elementary species (e. g., *Adalia* in Colorado). Further differentiation, involving partial sterility, may be illustrated by the *Basilarchia* species-cluster. This may be followed by the establishment, and isolation through complete sterility, of distinct types, or species in the strict sense of the term.

Evolution of color in the yellow and orange butterflies of the genus *Colias* involves white, which exists to-day in heterozygous condition in certain females. If the ancestors of *Colias* were white, as in Pierids generally, we have only to imagine a mutation in the male-producing germ cells of the original white females, by virtue of which white pigment was replaced by, or transmuted into, yellow. This would make all the males yellow, leaving all the females white, which is true of certain arctic species to-day.

A similar mutation affecting the germ cells of these white females, but introducing the factor for yellow into only half of them, would produce the heterozygous condition found in *C. philodice* and *C. eurytheme*. Pure yellow strains may readily be bred from such mixed stock, and hence, probably, it has come about that four fifths or nine tenths of the females of *C. philodice* in eastern United States are pure yellow.

Progressive mutations from yellow to orange and fiery orange, affecting first the male, then the female, have probably occurred in *Colias* in many part of the world, especially in warmer climates. Climatic conditions determine the amount of orange pigment in the cross between the orange *eurytheme* and the yellow *philodice*. This hybrid is larger and contains more orange when raised in summer than when bred in late fall and winter. *C. philodice* in this cross is a Mendelian recessive.

HEREDITY OF BRISTLES IN THE COMMON
GREENBOTTLE FLY, *LUCILIA SERICATA*
MEIG. A STUDY OF FACTORS GOVERN-
ING DISTRIBUTION¹

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IN a previous paper² I have given data showing that variation in the number of posterior dorso-central and acrostichal bristles of the common greenbottle fly, *Lucilia sericata* Meig., is determined by hereditary factors. Since the publication of that paper further evidence, bearing upon the nature of the hereditary factors involved, has been obtained.

Two general conclusions from the work may be stated as follows:

1. Reduction in bristles tends to affect the males more than the females, while additional bristles are found more often in the females.

2. Distribution as well as number of bristles is hereditary.

On account of very high mortality in these flies it has been impossible to make selections as might seem desirable. The results, however, furnish considerable evidence for the foregoing conclusions, and throw light, I believe, on the nature of factors governing distribution, such as spotting factors, for example.

Fig. 1 shows the mesonotum of *Lucilia sericata* with chaetotaxy normal. The bristles considered in my work are those lettered *A*, *B*, *C*, the post-acrostichals, and *A'*, *B'*, *C'*, the post-dorso-centrals.

¹ From the Entomological Laboratory of the Bussey Institution, Harvard University, No. 77.

² Whiting, P. W., "Observations on the Chaetotaxy of Calliphorinae," *Annals of the Entomological Society of America*, VI, 2.

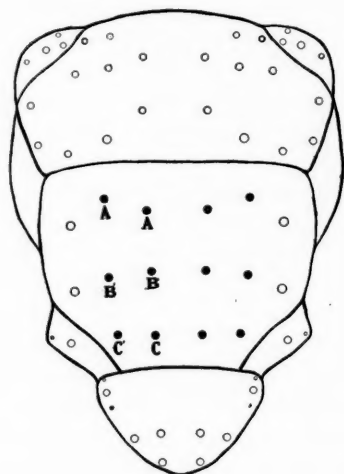


FIG. 1.

It is evident that these bristles form a group of twelve in four rows of three each.

This arrangement is recorded as 3, 3, 3, 3, the separation into rows being denoted by commas.

When one or two of the anterior bristles of a row are omitted, the row is denoted by 2 or 1, respectively.

In order to denote the omission of the second or third bristle when those anterior to it are not omitted, the normal positions of the bristles are recorded as a, b, c, from anterior to posterior. Thus a row lacking the second bristle would be called ac.

Addition of a supernumerary bristle into a row is denoted by ! inserted in the proper position between or in front of the letters denoting the normal bristles. Thus addition of a bristle in front of a row would be expressed by calling the row !abe.

Insertion of a supernumerary bristle between the normal rows is denoted by parentheses enclosing a, b, or c, according to the position of the bristle from anterior to posterior. Thus a definition as 3, (a), 3, 3, 3, would denote the addition of a bristle between the first left post-dorso-central and the first left post-aerostichal.

Additional bristles are usually smaller than the normal, but range all the way from microchaetae to the size of the normal macrochaetae. A small bristle is denoted by italics.

The progeny of a few wild females have been bred and counted since my previous paper.³ These have been

averaged with those recorded previously and the results given in Table I.

From this table it appears that progeny of normal mothers show a certain degree of variation in the direction both of loss and of acquisition of bristles; progeny of reduced mothers tend more toward reduction; and progeny of mothers bearing additional bristles tend more toward the addition of bristles. It is also evident that in

³ It is thought desirable to put on record a detailed account of these families as they furnish in themselves a few points of interest. This record is given below with the exception of the progeny of 1913-A, discussed in a later part of this paper.

1913-B, *L. sericata* ♀ = 3, ab, ab, 3, taken at Bussey Institution, May 6, 1913, gave

11 ♂♂ = 3, 3, 3, 3.	
1 ♂ = 3, 3, 3, 2.	
3 ♂♂ = 3, 2, 3, 3.	17 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, ac, 3.	1 ♀ = 3, 2, 3, 3.

1913-C, *L. sericata* ♀ = 3, 3, 2, 3, taken at Bussey Institution, May 6, 1913, gave

49 ♂♂ = 3, 3, 3, 3.	57 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, abc, 3.	1 ♀ = !abc, a!bc, 3, 3.
1 ♂ = 3, a!bc, a!bc, 3.	1 ♀ = 3, a!bc, 3, 3.
1 ♂ = 3, a!bc, 3, 3.	
1 ♂ = 3, !abc, 3, 3.	

In this case I attribute the additional bristles to the combination of factors introduced by the male. An example of this sort in which a reduced female produces offspring abnormal predominantly by addition is very unusual. There are, however, occasionally flies with extra bristles in reduced strains, a fact which may be explained by recombinations of factors or by mutation.

1913-F, *L. sericata* ♀ = 3, 3, 3, 3, taken at Bussey Institution, March 19, 1913, gave

24 ♂♂ = 3, 3, 3, 3.	19 ♀♀ = 3, 3, 3, 3.
from a mating of these were produced	
92 ♂♂ = 3, 3, 3, 3.	89 ♀♀ = 3, 3, 3, 3.
1 ♂ = 3, 3, a!bc, 3.	1 ♀ = 3, a!bc, 3, 3.

1913-D, *L. caesar* ♀ = 3, 2, 2, 3 (the chaetotaxy normal for this species), taken at Bussey Institution, May 5, 1913 gave

55 ♂♂ = 3, 2, 2, 3.	34 ♀♀ = 3, 2, 2, 3.
4 ♂♂ = 3, 1, 2, 3.	1 ♀ = ac, 2, 2, 3.
1 ♂ = 3, 2, b, 3.	
2 ♂♂ = 3, 1, 1, 3.	
1 ♂ = 3, 2, 1, 3.	
1 ♂ = 3, b, 2, 3.	

The flies of this mating are not averaged with the others, as it is possible that this species may be different in its variability from *L. sericata*. It is noteworthy, however, that here also reduction favors the male more than the female.

general reduction tends considerably to favor the males, while addition favors the females to a slight extent.

In my previous paper (p. 264) is given in detail a record of the progeny of a female *L. sericata* (1912-c) lacking both of the first and the right second post-acrostichal (3, 2, 1, 3). These were inbred to the third generation, in all cases brother being mated with sister in an attempt to analyze the stock as thoroughly as possible and to reduce heterozygosis of factors.⁴ Here again, due

⁴ Mr. Harold D. Fish has kindly furnished me the following note:

"The importance of mating sisters with brothers for a long series of generations in the experiments aimed to detect Mendelizing units of inheritance and analyze groups of them, quite generally seems to have been overlooked. As first shown by Castle ('03), random mating of the individuals of successive generations beyond F_1 tends to produce in each generation a population with the same per cent. of homozygosis and heterozygosis as is present in the F_1 generation, i. e., 25 per cent. of the individuals are homozygous for one factor of a given allelomorph pair, 25 per cent. homozygous for the other factor, and 50 per cent. heterozygous for both. Such a system of random matings often has been confused with the more restricted system of mating sisters with brothers.

"It is evident that if A and B are an allelomorph pair the F_2 zygotes, resulting from a mating of AA with BB , will be AA , $2AB$ and BB . Further, if these are all females and are mated in all possible ways with the same number and kinds of males, one sixteenth of the matings will be AA with AA , and one sixteenth will be BB with BB . One eighth of the matings, then, will be homozygous and produce only homozygous young, which, because of the restricted system of mating only sisters with brothers, will produce, in turn, only homozygous matings. The remaining matings, seven eighths of the total, will produce various proportions of homozygous and heterozygous offspring and matings. It is rather natural to assume that one eighth of these matings will be homozygous and seven eighths heterozygous. This would mean that the proportion of heterozygous matings between individuals of the F_n generation would be $(7/8)^{n-1}$. Accordingly one would expect an automatic increase in homozygosis. The expectation is justified although the figures are misleading.

"Dr. Raymond Pearl first published the figures exactly expressing the per cent. of automatic increase in homozygosis for paired allelomorphs, under the restriction of mating only sisters with brothers. This article appeared in the January, 1914, number of the AMERICAN NATURALIST. It is a correction of his paper in the October, 1913, number of the same periodical, in which he states in no uncertain terms that an automatic increase in homozygosis in obligate bisexual forms is impossible. When I read the October paper I was naturally much surprised, since, nearly a year before, during conversation with Mr. Whiting, the increasing per cent. of homozygous matings resulting from successive matings of sisters with brothers had been discussed. Of course, the per cent. of individuals in any generation, which are homozygous for one or the other of a pair of allelomorphs, is the same

to high mortality, selection as might have been desired has been impossible.

A detailed account of this strain is given in Table II. In recording any mating of this strain the letter *c* denoting the entire strain, is followed by F_1 , F_2 , etc., denoting the generation from which the mated flies have been chosen. This symbol is then followed by *a*, *b*, or *c*, denoting the first, second, or third mating, respectively, of the generation indicated. Thus mating cF_2b is the second mating of the second inbred generation of strain 1912—*c*. This method of recording matings has been followed throughout my work.

Several points of interest are to be noted in this strain but it is thought best to present the remaining data on reduced strains before proceeding to a discussion of this matter.

Strict inbreeding has been followed in the strain recorded below. In no case have there been either cousin-matings or outcrossings.

1913-A, *L. sericata* ♀ = 3, ac, ac, 3, taken at Bussey Institution, Forest Hills, Mass., May 6, 1913, gave

F_1

96 ♂♂ = 3, 3, 3, 3.
 1 ♂♂ = 3, ac, ac, 3.
 2 ♂♂ = 3, ac, 3, 3.
 2 ♂♂ = 3, 3, ac, 3.
 1 ♂♂ = 3, 2, ac, 3.
 4 ♂♂ = 3, 2, 3, 3.
 3 ♂♂ = 3, 3, 2, 3.

129 ♀♀ = 3, 3, 3, 3.
 1 ♀♀ = 3, ac, 3, 3.
 2 ♀♀ = 3, 2, 3, 3.

as the per cent. of the allelomorphic factors which are homozygous in the average individual of that generation. Because Dr. Pearl in his October paper referred frequently to the paper by Dr. E. M. East ('12) on "Heterozygosis in Evolution and Plant Breeding." I gave Dr. East my figure expressing the per cent. of homozygosis in successive generations resulting from matings of sisters with brothers. Dr. Pearl's correction followed a letter from Dr. East which pointed out the error of applying the mathematics of random matings in each generation to a case where sisters always had been mated with brothers. The percentages, as computed, were published by Dr. Pearl for the following generations: P_1 —100 per cent., F_1 —0 per cent., F_2 —50 per cent., F_3 —50 per cent., F_4 —62.5 per cent., F_5 —68.25 per cent., F_6 —75 per cent., F_7 —79.687 per cent., F_8 —83.594 per cent., F_9 —86.719 per cent., F_{10} —89.258 per cent. Previous to giving these figures to Dr. East I computed the number of generations necessary to reduce heterozygosis to less than one half of one per cent. and found this condition first realized in the F_{20} generation, which is 99.553 per cent. homozygous. The importance of these figures in work of this nature is quite obvious."

TABLE II
RECORD OF STRAIN 1912c, *L. sericata* ♀ (3, 2, 1, 3), TAKEN AT THE GARBAGE SCOW, BOSTON, AUGUST 8, 1912

Generations and Character of Matings	Progeny from Matings Recorded in First Column															
	Number of Flies Showing Bristles				Total Progeny				Bristles Lacking in "Decreased" Flies							
	Normal		Decreased		Increased		Total Progeny		Acrostichals				Dorso-centrals			
									1st		2d		3d			
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
F ₁ from mother = (3, 2, 1, 3).....	10	12	0	0	0	0	22	0	0	0	0	0	0	0	0	0
F ₂ from cF ₁ a = normal pair.....	10	7	0	0	0	0	17	0	0	0	0	0	0	0	0	0
F ₂ from cF ₁ b = normal pair.....	42	39	2	2	2	0	87	1	0	0	3	0	0	2 (2d)	0	0
F ₂ from cF ₁ c = normal pair.....	55	62	10	9	1	0	137	16	7	0	1	0	1	1 (2d)	1	0
F ₂ from cF ₂ a = normal male X 2 normal females.....	163	170	6	6	2	7	354	1	0	4	2	0	0	0	3.5 (2d)	8
F ₂ from cF ₂ b = normal pair.....	92	85	0	1	11	4	193	0	0	0	1	0	0	0	2 (3d)	0
Totals.....	372	375	18	18	16	11	810	18	7	4	7	0	1	3	10.5	12

F₂

from $AF_1a = \begin{cases} \sigma = 3, ac, 3, 3. \\ \varphi = 3, 2, 3, 3. \end{cases}$

24 $\sigma\sigma = 3, 3, 3, 3.$
 11 $\sigma\sigma = 3, ac, ac, 3.$
 13 $\sigma\sigma = 3, ac, 3, 3.$
 9 $\sigma\sigma = 3, 3, ac, 3.$
 2 $\sigma\sigma = 3, abc, ac, 3.$
 1 $\sigma = 3, 3, abc, 3.$
 1 $\sigma = 3, 1, 1, 3.$
 3 $\sigma\sigma = 3, ac, 2, 3.$
 5 $\sigma\sigma = 3, 2, ac, 3.$
 1 $\sigma = 3, 2, 2, 3.$
 5 $\sigma\sigma = 3, 2, 3, 3.$
 2 $\sigma\sigma = 3, 3, 2, 3.$
 1 $\sigma = 3, acc, 3, 3.$

53 $\varphi\varphi = 3, 3, 3, 3.$
 2 $\varphi\varphi = 3, ac, ac, 3.$
 5 $\varphi\varphi = 3, 3, ac, 3.$
 1 $\varphi = 3, ac, abc, 3.$
 1 $\varphi = 3, ac, 2, 3.$
 2 $\varphi\varphi = 3, 3, abc, 3.$
 1 $\varphi = 3, abc, 3, 3.$
 1 $\varphi = 3, abc, 2, 3.$
 2 $\varphi\varphi = 3, 2, 2, 3.$
 1 $\varphi = 3, 3, 2, 3.$
 1 $\varphi = 3, 3, a!c, 3, 3.$
 1 $\varphi = 3, a!bc, 3, 3.$

F₃

from $AF_2a = \sigma$ and $\varphi = 3, ac, ac, 3.$ Pair segregated July 12; larvae

July 25.

$\sigma\sigma$ $\varphi\varphi$
 6 35 = 3, 3, 3, 3.
 42 18 = 3, ac, ac, 3.
 9 18 = 3, ac, 3, 3.
 16 12 = 3, 3, ac, 3.
 5 2 = 3, ac, 2, 3.

$\sigma\sigma$ $\varphi\varphi$
 7 2 = 3, 2, ac, 3.
 10 4 = 3, 2, 2, 3.
 7 7 = 3, 2, 3, 3.
 5 7 = 3, 3, 2, 3.
 1 0 = 3, ac, a, 3.

from $AF_2b =$

$\sigma = 3, ac, 2, 3.$
 $\varphi = 3, abc, 2, 3.$

Pair segregated July 12; larvae July 25.

$\sigma\sigma$ $\varphi\varphi$
 16 45 = 3, 3, 3, 3.
 34 9 = 3, ac, ac, 3.
 8 9 = 3, ac, 3, 3.
 7 11 = 3, 3, ac, 3.
 8 0 = 3, ac, 2, 3.
 9 1 = 3, 2, ac, 3.
 3 0 = 3, 2, 2, 3.
 2 1 = 3, 2, 3, 3.

$\sigma\sigma$ $\varphi\varphi$
 4 1 = 3, 3, 2, 3.
 0 1 = 3, abc, ac, 3.
 0 3 = 3, 3, abc, 3.
 0 3 = 3, abc, abc, 3.
 1 0 = 3, b, 3, 3.
 1 0 = 3, ac, abc, 3.
 0 1 = 3, abc, 3, 3.

F₄

from $AF_3a = \begin{cases} \sigma = 3, ac, a, 3, \text{ from } AF_2a. \\ \varphi = 3, ac, ac, 3, \text{ larvae August 20.} \end{cases}$ Pair segregated August 14;

$\sigma\sigma$ $\varphi\varphi$
 6 32 = 3, 3, 3, 3.
 24 11 = 3, ac, ac, 3.
 4 20 = 3, ac, 3, 3.
 6 13 = 3, 3, ac, 3.
 9 6 = 3, ac, 2, 3.
 6 7 = 3, 2, ac, 3.
 3 4 = 3, 2, 2, 3.

$\sigma\sigma$ $\varphi\varphi$
 4 7 = 3, 2, 3, 3.
 1 5 = 3, 3, 2, 3.
 1 0 = 3, ac, 1, 3.
 0 1 = 3, ac, 3, 3.
 1 0 = 3, ac, bec, 3.
 0 1 = 2, 2, 2, 3.
 0 1 = 3, 3, abbc, 3.

from $AF_3b = \sigma$ and $\varphi = 3, 2, ac, 3,$ from $AF_2a.$ Pair segregated August 13; larvae August 20.

$\sigma\sigma$ $\varphi\varphi$
 0 18 = 3, 3, 3, 3.
 10 3 = 3, ac, ac, 3.
 4 5 = 3, ac, 3, 3.
 1 2 = 3, 3, ac, 3.
 13 3 = 3, ac, 2, 3.

$\sigma\sigma$ $\varphi\varphi$
 13 2 = 3, 2, ac, 3.
 6 2 = 3, 2, 2, 3.
 1 7 = 3, 2, 3, 3.
 1 4 = 3, 3, 2, 3.

from $AF_3c = \sigma$ and $\varphi = 3, 2, 2, 3,$ from $AF_2a.$ Pair segregated August 13; larvae August 25.

♂♂	♀♀	♂♂	♀♀
6	15 = 3, 3, 3, 3.	2	15 = 3, 2, 3, 3.
10	7 = 3, ac, ac, 3.	3	8 = 3, 3, 2, 3.
11	7 = 3, ac, 3, 3.	0	1 = ac, 1, 2, ac.
10	12 = 3, 3, ac, 3.	1	0 = 3, 2, acc, 3.
8	3 = 3, ac, 2, 3.	2	1 = 3, acc, ac, 3.
7	7 = 3, 2, ac, 3.	1	0 = 3, acc, 3, 3.
5	4 = 3, 2, 2, 3.		

from $AF_2d = \delta$ and $\varphi = 3, ac, ac, 3$, from AF_2a . Pair segregated August 13; male died August 18 and another with same chætotaxy put in; larvæ September 1.

♂♂	♀♀	♂♂	♀♀
0	3 = 3, 3, 3, 3.	1	1 = 3, ac, 2, 3.
1	2 = 3, ac, 3, 3.	1	0 = 3, 3, aabe, 3.
1	1 = 3, 3, ac, 3.		

The record of 1913-A, recorded in tabular form is given in Table III.

We are now in a position to consider the nature of reduction of bristles in *Lucilia sericata*.

It is evident from Table I (record of first generation flies), that reduction and addition of bristles are both hereditary. It is further evident from Table III, (inbred strain), that reduction yields readily to selection. This effect may be expressed by making the number of bristles lost the numerator of a fraction of which the denominator is the number of bristles normal. We then have a ratio for each generation of 1913-A as follows:

$$F_1 \cdot \frac{18}{2892} = 0.006 \pm .010, \quad F_3 \cdot \frac{435}{4692} = 0.093 \pm .003,$$

$$F_2 \cdot \frac{99}{1788} = 0.055 \pm .004, \quad F_4 \cdot \frac{532.5}{5100} = 0.104 \pm .003.$$

It may be readily seen by glancing at these figures that selection has a very rapid effect. It also appears that as we pass from F_1 to F_4 the effect of selection gradually diminishes. This may be expressed by dividing the above decimals for each generation by that of the preceding generation.

$$\frac{F_2}{F_1} = \frac{0.055}{0.006} = 9.16, \quad \frac{F_3}{F_2} = \frac{0.093}{0.055} = 1.69,$$

$$\frac{F_4}{F_3} = \frac{0.104}{0.093} = 1.11.$$

The reason for this decrease in the effect of selection in the later generations is that as the selection advances the majority of the flies become reduced in two bristles only.

TABLE III
RECORD OF STRAIN 1913-A, *L. sericata* ♀ (3, ac, ac, 3) TAKEN AT THE BUSSEY INSTITUTION, FOREST HILLS, MASS., MAY 6, 1913

Generations and Character of Matings	Progeny from Matings Recorded in First Column																	
	Number of Flies Showing Bristles				Decreased and Increased in Same Individual				Total Prog- eny	Bristles Lacking in "Decreased" Flies								
	Normal		Decreased		Increased		Acrostichals						Dorso- centrals		Bristles Added in "Increased" Flies			
							Acrostichals											
							1st			2d		3d						
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	Small 2d Acrosti- chals		
F ₁ from mother = (3, ac, ac, 3).....	96	129	13	3	0	0	0	0	241	8	2	7	1	0	0	0	0	0
F ₂ from AF ₁ a = { ♂ = 3, ac, 3, 3, ♀ = 3, 2, 3, 3.....	24	53	53	16	0	1	1	1	149	19	7	58.5	14.5	0	0	0	1	2
F ₃ from AF ₂ a = ♂ and ♀ = 3, ac, ac, 3.	6	35	102	70	0	0	0	0	213	34	26	123	70	1	0	0	0	0
F ₃ from AF ₂ b = { ♂ = 3, ac, 2, 3, ♀ = 3, abc, 2, 3.....	16	45	77	40	0	0	0	0	178	30	3	101.5	45.5	1	0	0	0	12
F ₄ from AF ₃ a = { ♂ = 3, ac, a, 3, ♀ = 3, ac, ac, 3, from AF ₃ a.....	6	32	58	75	0	0	1	1	173	28	36	76	69.5	0	0	1 (1st)	1	0
F ₄ from AF ₃ b = ♂ and ♀ = 3, 2, ac, 3. from AF ₃ a.....	0	18	49	28	0	0	0	0	95	40	20	51	18	0	0	0	0	0
F ₄ from AF ₃ c = ♂ and ♀ = 3, 2, 3, from AF ₃ a.....	6	15	56	64	0	0	4	1	146	31	43	62	46	0	0	2 (2d)	4	1
F ₄ from AF ₃ d = ♂ and ♀ = 3, ac, ac, 3, from AF ₃ a.....	0	3	3	4	1	0	0	0	11	1	1	3	4	0	0	0	1	0
Totals.....	154	330	411	300	1	1	6	3	1,206	191	138	482	268.5	2	0	3	7	3

Rarely does a fly occur lacking more than two. In the few cases in which three or more bristles are lacking, the absence of the third acrostichals or of the dorso-centrals is as frequent as the absence of first and second acrostichals. Why this should be is difficult to understand, as it would be expected that both first and both second post-acrostichals might frequently be lacking in the same fly, especially as flies asymmetrical for the loss of these bristles are common.

A further point of interest lies in the fact that not only is *number* of bristles a hereditary matter, but their *distribution* is also hereditary. Thus from Table I (first-generation flies) we see that in general the first post-acrostichals tend to be reduced more than the second. This may be expressed as a fraction:

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}} = \frac{40.5}{34} = 1.19.$$

It is possible that this tendency to reduce the first post-acrostichal more than the second is evidence of relationship to *L. caesar* Linn., in which the absence of the former and the presence of the latter is the normal condition. Strain 1913—A (Table III), however, gives

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}} = \frac{329}{750} = 0.43.$$

Considering the reduction in the first post-acrostichals separately, we may express the effect of selection as follows:

Parents. Matings.	1st post-acros. lacking.	Offspring.
		First post-acros. lacking. First post-acros. normal (2 per fly).
A	0(?)	$\frac{10}{482} = 0.021 \pm .004.$
AF ₁ a	1	$\frac{26}{298} = 0.087 \pm .011.$
AF ₂ a	0	$\frac{60}{426} = 0.141 \pm .002.$
AF ₂ b	2	$\frac{33}{356} = 0.093 \pm .010.$

AF_3a	0	$\frac{64}{346} = 0.185 \pm .014.$
AF_3b	2	$\frac{60}{190} = 0.316 \pm .023.$
AF_3c	4	$\frac{74}{292} = 0.253 \pm .017.$

From these figures it is readily seen that reduction in the first post-acrostichals is not entirely consistent with the direction of selection.

Let us test the same matter for reduction in the second post-acrostichals.

Parents Matings	1st post-acros. lacking	Offspring.
		First post-acros. lacking. First post-acros. normal (2 per fly)
A	2(?)	$\frac{8}{482} = 0.017 \pm .004.$
AF_1a	1	$\frac{63}{298} = 0.211 \pm .016.$
AF_2a	4	$\frac{193}{426} = 0.453 \pm .016.$
AF_2b	1.5	$\frac{147}{356} = 0.413 \pm .018.$
AF_3a	4	$\frac{145.5}{346} = 0.420 \pm .179.$
AF_3b	2	$\frac{69}{190} = 0.363 \pm .023$
AF_3c	0	$\frac{108}{292} = 0.370 \pm .019.$

In this case also the results are not consistent with the direction of selection, although there is better agreement here than in the case of the first post-acrostichals. This is probably due to the fact that the numbers are larger. As regards the irregularities that do occur, I consider them as evidence of recombinations of multiple factors, insofar as they are not due to probable error.

1912—*c* (Table II) is a strain that especially tends to lack the first post-acrostichals. Thus for the entire strain

$$\frac{\text{First post-acrostichals lacking}}{\text{Second post-acrostichals lacking}} = \frac{25}{11} = 2.27.$$

In the 137 offspring of a single mating of this strain, cF_1c , there are 23 first post-acrostichals lacking, showing that it is due to this mating especially that the strain is so lacking in first post-acrostichals.

It can not as yet be said that the factors governing the first post-acrostichals are altogether independent of those governing the second. That a certain degree of independence obtains is evident from a comparison of the ratio of reduction in first to reduction in second post-acrostichals in flies in general (Table I), with the same ratio for strain 1913—A. In the former case we have $40.5/34$ or 1.19. In the latter we have $329/750$, or 0.43. In order to establish the independence of the factors underlying these two tendencies it will be necessary to obtain, either by selection from a strain showing both tendencies or by breeding from wild stock, two strains, one tending to lack the first while retaining the second, and the other tending to lack the second while retaining the first.

A point of interest in strain 1913—A is the presence of twelve small second post-acrostichals in the progeny of AF_2b in which the female had one of these reduced to half size. The progeny of AF_2a in which there was total absence of these bristles showed either presence or absence of the same but no reduced bristles. In F_2 , however, we have eight reduced bristles. The occurrence of these small bristles in the progeny of certain matings is taken as an indication of recombinations of multiple factors, but the numbers are too small to establish this with certainty.

A glance at the tables shows that third post-acrostichals are rarely lacking. These are normally present in all related species, while in a few,—*Cynomyia mortuorum*, *Musca domestica*, *Pseudopyrellia cornicina*, and others, there is normally but one post-acrostichal, and this is always the last.

Posterior dorso-centrals are very rarely absent. Thus in the 2,273 flies recorded in Table I only one had a single post-dorso-central missing. Reduction in post-acrosti-

chals among these is 79.5. Among the 1,206 flies of strain 1913—*A* there are but three post-dorso-centrals gone. This latter is a highly reduced strain as regards post-acrostichals, lacking 1,081. This great reduction in acrostichals seems not appreciably to have affected the dorso-centrals, a fact which argues for the independence of the factors controlling the distribution of these two sets of bristles.

Thus for flies recorded in Table I we have

$$\frac{\text{Post-acrostichals lacking}}{\text{Number of Flies}} = \frac{79.5}{2273} = 0.03.$$

One post-dorso-central lacking.

For flies in strain 1913—*A* (Table III) we have

$$\frac{\text{Post-acrostichals lacking}}{\text{Number of Flies}} = \frac{1081}{1206} = 0.89.$$

Three post-dorso-centrals lacking.

Among the 3,238 flies recorded in Tables I and III only four post-dorso-centrals are lacking, while among the 810 flies of strain 1912—*c* (Table II) there are 13.5 lacking. The lack of post-acrostichals in this latter strain is 37. There are 9.5 dorso-centrals lacking in the progeny of the trio, *cF₂a*, among which there are only seven post-acrostichals lacking.

Thus we see that lack of post-dorso-centrals is in no way correlated with lack of post-acrostichals, but is evidently governed by distinct factors.

VARIATION BY ADDITION OF BRISTLES

A strain of *Lucilia sericata*, 1913—*E*, showed some interesting variations chiefly in the direction of addition of bristles. The mother was normal (3, 3, 3, 3), taken at the Bussey Institution, March 19, 1913. The detailed account of the strain follows:

$$\begin{array}{l} F_1 \\ \begin{array}{cc} \sigma\sigma & \text{♀♀} \\ 38 & 43 = 3, 3, 3, 3. \\ 1 & 0 = 3, 3, \text{ab!e}, 3. \end{array} \\ F_2 \\ \text{from } EF_1a = \begin{cases} \sigma = 3, 3, \text{ab!e}, 3. \\ \text{♀} = 3, 3, 3, 3. \end{cases} \end{array}$$

$\sigma\sigma$	$\varphi\varphi$
69	76=3, 3, 3, 3.
1	0=ab!e, 3, 3, 3.
0	1=!abe, 3, 3, !abe.

F₃
from EF₂a = σ and φ = 3, 3, 3, 3.

$\sigma\sigma$	$\varphi\varphi$
318	251=3, 3, 3, 3.
13	51=!abe, 3, 3, !abe.
1	4=!abe, 3, 3, 3.
6	6=3, 3, 3, !abe.
1	3=3 (a), 3, 3, 3.
5	2=3, 3, 3 (a), 3.
3	5=3, 3, a!be, 3.
1	0=3, a!be, abe!, 3.
1	0=3, 3, 3, a!be.
1	0=3, 3, 3, ab!e.
1	0=!abe, a!be, 3, 3.
1	0=3, 3, 3 (b), 3.
1	1=3, a!be, a!be, 3.
1	0=!a!be, !a!be, !a!be, !a!be.
0	1=3 (b), 3, a!be, a!be.
0	2=!a!be, 3, 3, !abe.
0	1=!abe, 3, a!be, !abe.

F₄

from EF₃a = { σ = 3, 3, 3, 3.
 φ = 3, 3, a!be, 3.

Pair segregated, July 22; larvæ July 30.

$\sigma\sigma$	$\varphi\varphi$	$\sigma\sigma$	$\varphi\varphi$
191	100=3, 3, 3, 3.	1	0=!abe, 3, abe!, !abe.
25	43=!abe, 3, 3, !abe.	2	0=3, abe!, 3, 3.
4	3=!abe, 3, 3, 3.	1	0=!abe (a), 3, 3.
0	1=3, 3, 3, !abe.	1	0=3 (a), 3, 3 (a), 3.
0	1=!abe, a!be, 3, !abe.	1	1=!abe, 3, 3 (a), !abe.
1	2=!abe, 3, a!be, !abe.	0	1=!be, 3, 3, 3.
0	2=!abe, a!be, a!be, !abe.		

from EF₃b = σ and φ = 3, 3, 3, 3. Pair segregated August 22.

$\sigma\sigma$	$\varphi\varphi$	$\sigma\sigma$	$\varphi\varphi$
41	57=3, 3, 3, 3.	2	0=3, a!be, 3, 3.
0	1=3, a!be, 3, !abe.	0	1=!abe, 3, 3, !abe.
1	0=3, abe!, 3, 3.	0	1=!abe, a!be, a!be, !abe.

A summary of this strain is given in Table IV.

The points of interest to be noted in this table are as follows:

There are many supernumerary bristles in the flies of this strain.

The number of bristles added in the progeny of any mating is very variable and has no consistent relation to the visible character of the parents.

Addition of bristles tends very much to favor the females, reduction still affecting the males.

Despite the high ratio of bristles added, there are

TABLE IV
RECORD OF 1913 *E. STRAIN*, *L. sericata* ♀ (3, 3, 3) TAKEN AT THE BUSSEY INSTITUTION, FOREST HILLS, MASS., MARCH 19, 1913

Generation and Character of Matings	Progeny from Matings Recorded in First Column											
	Number of Flies Showing Bristles						Total Progeny			Bristles Lacking in "Decreased" Flies		
	Normal		Decreased		Increased		Decreased and Increased			Increased		Bristles Added in "Increased" Flies
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
F ₁ from mother = (3, 3, 3).....	38	43	0	0	1	0	0	0	0	0	1	0
F ₂ from EF ₁ a = { ♂ = 3, 3, 3, ab! c, 3, ♀ = 3, 3, 3, 3.....	69	76	0	0	1	1	0	0	0	0	1	2
F ₃ from EF ₂ a = normal pair.....	318	251	3	1	44	91	1	0	4	0.5	75	170
F ₄ from EF ₃ a = { ♂ = 3, 3, 3, 3, ♀ = 3, 3, 3, a! bc, 3.....	191	100	0	0	36	53	0	1	0	1	73	111
F ₄ from EF ₃ b = normal pair.....	41	57	0	0	3	3	0	0	0	0	3	8
Totals.....	657	527	3	1	85	148	1	1	4	1.5	153	291

nevertheless a few flies in the strain in which bristles are lacking.

Bristles normally present may be lacking in individuals having additional bristles.

GENERAL SUMMARY AND CONCLUSIONS

Taking a general summation of all the bred material of *Lucilia sericata*, we find that reduction affects the males while addition affects the females. Of the 5,367 flies bred, 2,708 are males and 2,659 are females, giving practical equality.

Reduction in the males is 748.5 bristles, while in the females it is only 455.5 bristles. As has been noted before the degree of reduction in the females is increased by the later generations of strain 1913—A, by reason of the fact that reduction rarely goes beyond the loss of two bristles in a single fly. Thus when most of the flies of a population become reduced to this extent it is evident that reduction in the males would be but slightly in advance of that in the females.

There are 210 bristles added in the males, while there are 343 added in the females. Thus addition affects the females more than the males. These figures for bristles added represent number of bristles, and thus no distinction is made between bristles of large and bristles of small size.

I wish to express my appreciation for the advice and criticism offered me in this work by Professor W. M. Wheeler, Messrs. H. D. Fish, S. G. Wright, and C. C. Little.

PHYSIOLOGICAL CORRELATIONS AND CLIMATIC REACTIONS IN ALFALFA BREEDING¹

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CLIMATIC REACTIONS

To the worker who attempts to apply the recognized laws of heredity to the actual operations of plant improvement many difficulties arise which heretofore have been largely avoided by students of pure genetics. Color and form characters are but little affected by the immediate ordinary environment and hence, for the sake of simplicity, are usually chosen by investigators of heredity. To the economic breeder, however, such characters are of but little consequence except in so far as they indicate phyletic relationships. Of greater importance to the breeder are those differences in yield and quality which are the results of inherited, invisible, physiological powers within the plants, whereby each variety may respond differently in manner or degree to the same environmental stimulus.

Those hereditary units which have to do with vegetative vigor, heat, cold and drought resistance, time of maturity, chemical structure, reproductive strength, etc., are as yet but little understood. This is largely due to the difficulty of exact experiments concerning them. This difficulty is occasioned by the complexity of the reactions of these hereditary forces with the external environment, and also by the direct influence of the development of one part of the plant upon that of some other part. The plant at maturity presents the resultant of its environmental reactions during development. The nature of these reactions

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is determined by the structure of the vital forces within. These differences in vital structure may or may not be accompanied by visible morphological differences. Such cases of correlation have been known and used in selecting for qualities which they were thought to indicate. The much quoted example of the supposed correlation between the short-haired rachilla and high brewing quality in barley is a case in point. It has been found, however, that, whereas, in one strain or race the correlation may hold, in another, the two characters are in no way related. Another case of similar nature is the coupling of cob and pericarp color in certain varieties of corn and their complete independence in others. Many other examples could be adduced to show that the coupling of two characters in a given race of plants is no indication that these same characters are inseparably linked in all races of the same species. These facts have greatly reduced the value formerly ascribed to gametic correlations in plant breeding. Under our present knowledge, therefore, we must depend, for the most part, upon direct experimentation, rather than correlations, to discover the hereditary physiological characters of the varieties with which we are working. Any additional light, therefore, which may be had concerning the nature of such characters, together with methods for the study of the behavior of the same in their relation to each other and to their physical surroundings, will have not only a scientific value, but will also fill a distinct practical need.

As an illustration of such a study we may now examine the data concerning the development, yield and chemical composition of forty-four regional varieties of alfalfa which were grown on the Experiment Station Farm at Phoenix, Arizona, during the season of 1910. In the case of this plant, which occupies the ground throughout the year and from which six or seven crops may be harvested during the growing period, the climatic factors include a long series of variations coincident with the changing seasons. Now, since every variety consists of its own pecul-

lar complex of hereditary physiological forces, each sensitive in its own manner and degree to the impinging external stimuli, it is not surprising that the resultant (the gross climatic reaction) should be sharply different in the several varietal groups.

The unequal effects upon the vegetative growth of the different varieties brought about by the climatic changes which occurred during the course of the summer may be exhibited by calculating the place variation in yield. This is best shown by correlating the first with each of the following cuttings throughout the season. The result is a definite curve, beginning and ending high with a strong sag in the middle.

TABLE I

PLACE VARIATION IN YIELD

Cuttings	1 and 2	1 and 3	1 and 4	1 and 5	1 and 6
Correlation.	$+ .75 \pm .04$	$+ .68 \pm .05$	$+ .33 \pm .09$	$+ .36 \pm .09$	$+ .58 \pm .07$

These figures indicate the presence of some disturbing factor which reached its maximum intensity during the fourth and fifth cuttings, and to which certain plots were more sensitive than others. The average period through which the growth of these two crops extended was June 22 to August 27. The fact that these dates include the hottest portion of the summer strongly suggests temperature as the disturbing factor.

The mean maximum temperature, mean minimum relative humidity and the correlation between yield and water supplied are given in the following table:

TABLE II

TEMPERATURE, RELATIVE HUMIDITY AND WATER SUPPLY

Cutting	Dates Including Average Periods of Growth	Mean Maximum Temperature ° F.	Mean Minimum Relative Humidity	Correlation Between Yield and Water Supply
1	From March 23 to April 23	82.8	27.00	
2	From April 23 to May 23	93.8	23.00	$-.09 \pm .10$
3	From May 23 to June 22	103.6	20.40	$+.05 \pm .10$
4	From June 22 to July 23	104.8	25.26	$+.40 \pm .09$
5	From July 23 to August 27	104.4	30.00	$+.21 \pm .10$
6	From August 27 to October 5	102.0	25.18	$-.04 \pm .10$

That the relative humidity had little to do with yield is shown by the fact that the highest averages for this factor occurred on the first and fifth cuttings which were the highest and lowest in yield, respectively.

Although it was intended to give each plot approximately the same amount of water for each cutting, unevenness in the slope made this impossible. The average amount of water applied to each cutting was 6.28 inches with an average standard deviation of 1.54 inches. Now, taking cognizance of this variation in the water supply, we find that its effect upon the yield was only appreciable in the fourth and fifth cuttings. Records were not made of the water supplied to the first cutting, but after that time they are complete. By reference to Table II it will be observed that these correlations in the second, third and sixth cuttings are so small as to be negligible, but in the fourth and fifth cuttings they are sufficiently large to indicate that this factor was of some importance in governing the yields. These results may be interpreted as meaning that approximately 6.28 inches of water were ample for each cutting during the cooler weather of spring and fall. That too much was not given at these seasons, however, is shown by the absence of large minus correlations. Factors other than water supply, therefore, governed the yields during these periods. Hot, dry weather came on during the growth of the third cutting, but the amount of water supplied plus the winter and spring surplus left in the soil was ample to mature the crop. With the continued high demand for water during the hot weather of July and August, the surplus having been exhausted and the summer rains helping but little, six and one fourth inches was not sufficient. There was, therefore, marked suffering for water, which was reflected in the yields of those plots that received slightly more or less of irrigation than the others.

It would seem, therefore, that high temperature and a slight deficiency of water were the disturbing factors in

the relative yields of the varieties tested, and that certain ones were more sensitive than others to these influences.

If we turn to the relation between stand and yield, we shall again find a strong disturbance of the normal correlation as shown in the following:

TABLE III
CORRELATION BETWEEN STAND AND YIELD

Cutting	1st	2d	3d
Correlation	+ .78 \pm .04	+ .55 \pm .07	+ .47 \pm .08
Cutting	4th	5th	6th
Correlation	+ .54 \pm .07	+ .10 \pm .10	+ .70 \pm .05.

The exceptionally low coefficient of the fifth cutting was due to the low yields on the part of plots which had good stands but were relatively inactive during the hot weather and partial water famine which occurred at this period. On the other hand, certain plots through their resistance to heat and consequent activity at this period, overcame to a large extent their handicap of poor stands, and nearly obliterated the usual plus correlation between stand and yield.

The data thus studied *en masse* indicate at least two physiological groups which are unequally sensitive to the climatic changes which occur in the course of a growing season, and whose reactions were sufficiently strong to change almost completely the order of the productivity of the plots. In order to test this conclusion let us turn to the individual plots and endeavor to discover and classify the physiological varieties indicated above.

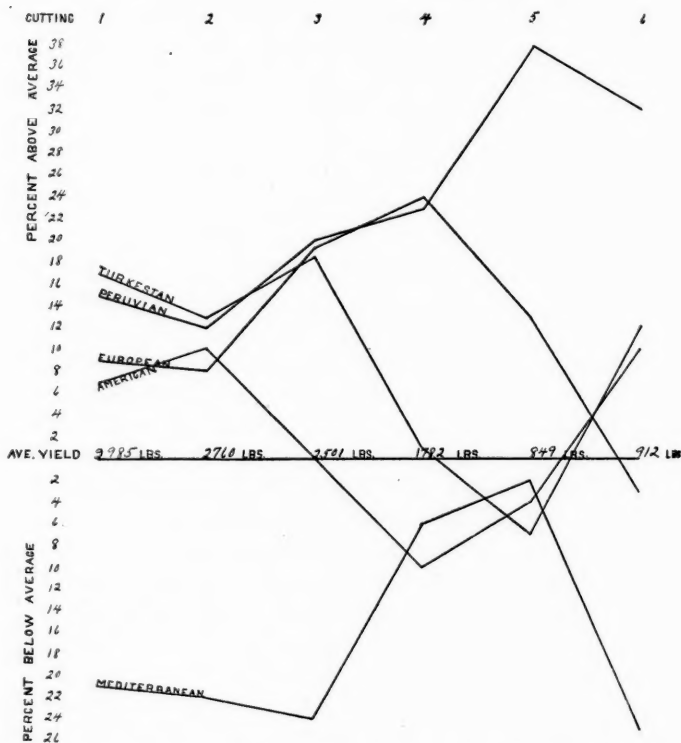
If, now, we arrange the forty-four regional strains according to their morphological characters and geographical origin, we shall have five more or less distinct groups as follows: Mediterranean, Peruvian, European, American and Turkestan. The behavior of these varietal groups through the course of six cuttings during the summer of 1910 substantiates the conclusions already drawn and illustrates the sharp differences in climatic reactions which may be observed in the several varieties of a single species.

Morphologically the Mediterranean and Peruvian alfalfas are so distinct in type that any one at all familiar with the different kinds of alfalfa would recognize them at a glance, whether a whole field or a single plant be observed. The presence of yellow or greenish blue flowers also determines a variety to be of northern origin with mixtures of falcata characters, which usually carry with them resistance to cold and drought. Otherwise, the Turkestan, American and European types are so nearly alike that only an expert would recognize them in mass culture. The individual variations within these three types intergrade to such a degree that one could scarcely assume to judge, from the observation of a single plant, the type prevailing in the field from which it originated. The three types, however, differ markedly in their physiological reactions as we shall presently see. The distinctions, in this regard, as exhibited on our plots, are not nearly so marked between the American and Turkestan alfalfas as between these two types, on the one hand, and the European, on the other. However, in northern climates where winter resistance enters as a potent factor, the Turkestan alfalfa exhibits greater hardiness than the American form, and, therefore, is able to maintain a more perfect stand through seasons of extreme frost.

When grown under Arizona conditions, the average yields of each of these five type groups present seasonal curves at once striking in their diversity and contrasts. These differences are exhibited more easily by plotting the average of all the plots as a straight line, and the average of the different groups as percentages of the total average above and below the general average line.

In observing Fig. 1, we are first impressed with a marked similarity in the performance of the European and Mediterranean alfalfas, on the one hand, and the American and Turkestan on the other, and also with the striking differences exhibited between the two groups. Although the average yield of the European plots greatly exceed that of the Mediterranean plots, the shapes of their respective

curves are almost exactly alike, the greatest relative yield of each being in the heated part of the summer after the beginning of the water famine. In like manner, the American and Turkestan varieties made similar relative yield curves, that for the Turkestan being slightly above the curve for the American strains. Here, however, the



RELATIVE YIELD OF REGIONAL VARIETIES BASED ON THE AVERAGE OF ALL PLOTS AS 100 PER CENT.

curves bend strongly downward in mid and late summer, as if these types were much less resistant to the accumulative effects of drought and heat. In fact, it would seem that during the hot period included within the fifth cutting

(July and August), the American and Turkestan varieties were comparatively inactive, yielding only about eight hundred pounds of dry hay per acre, as against more than a ton and a half each on the first cutting. The relative yield curve for the Peruvian type stands separate and distinct from the others. Although here, as with other varieties, the yield declines with the advance of the season, the persistence and vigor with which this strain resisted the summer heat and drought caused it to gain rapidly on the other varieties in relative yield throughout the season until the very last cutting, when there was a slight decline.

Disregarding the shape of the curves we may now notice the total yield for the season. In this respect the different regional varieties take the following relative order: Peruvian, European, Turkestan, American and Mediterranean. It is here noticeable that, though the European and Mediterranean varieties have similar seasonal yield curves, they are not contiguous in the arrangement based on total yields. This is a result of a marked difference in the stand maintained by the two varieties which averaged ninety-two per cent. for the former and seventy-four per cent. for the latter. In their ability to maintain stand, the Peruvian, European, Turkestan and American varieties were about equal, averaging 92, 92, 93 and 94 per cent., respectively. The lack of stand on the part of the Mediterranean alfalfas was not due to the poor quality of the original seed, for all of these plots once had perfect stands. This behavior is also in accordance with the records of other fields of Mediterranean alfalfa in the southwest, which have come under the observation of the writer. The explanation of the weakness of the Mediterranean and corresponding strength of the otherwise similarly reacting European alfalfa in maintaining stand under Arizona conditions is a subject for further careful physiological study.

The recognition, analysis, and calibration of these differences of the physiological reactions of varieties are thus seen to become a first essential in the study of climatic adaptation, and form the basis for rational procedure in the choice of varieties and in selective breeding for the improvement of the same.

CORRELATIONS

In the improvement of varieties of plants, quality is often as important as quantity of yield. This is especially true in a forage crop, such as alfalfa. Since nitrogen, next to fat, is the most expensive of the necessary food constituents, it may be taken as the measure of quality. Commercial buyers judge alfalfa hay by its purity, odor, color and percentage of leaves retained in curing and baling. The value of the leaves lies in their relatively high nitrogen content and the consequent increased food value which they impart to the hay. Expressed quantitatively, the correlations between the nitrogen content of the hay and the percentage of leaves for the six cuttings were as follows:

TABLE IV

CORRELATION BETWEEN NITROGEN CONTENT OF HAY AND PER CENT. OF LEAVES

Cutting	1st	2d	3d
Correlation	$+.46 \pm .08$	$+.61 \pm .06$	$+.72 \pm .05$
Cutting	4th	5th	6th
Correlation	$+.68 \pm .05$	$+.61 \pm .06$	$+.52 \pm .07$

That the final value of the hay is markedly dependent upon the composition as well as the percentage of leaves is shown by the following high and fairly uniform correlation between the nitrogen content of the hay and the nitrogen content of the leaves:

TABLE V

CORRELATION BETWEEN NITROGEN CONTENT OF HAY AND NITROGEN CONTENT OF LEAVES

Cutting	1st	2d	3d
Correlation	$+.69 \pm .05$	$+.73 \pm .05$	$+.42 \pm .08$
Cutting	4th	5th	6th
Correlation	$+.67 \pm .06$	$+.85 \pm .03$	$+.74 \pm .05$

If, now, we have shown that the quality of the hay depends primarily upon the percentage and composition of the leaves, we may proceed to investigate those factors which indirectly modify the feeding value by influencing the amount or character of these organs.

The factors most profoundly affecting the percentage of leaves were yield, height and stage of maturity at which the cutting was made. Local or varietal forces were

sufficiently constant to hold the place variation of this character to the plus side of the equation for four out of five determinations made, as is seen in the following table:

TABLE VI

PLACE VARIATION IN PERCENTAGE OF LEAVES					
Cutting	1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
Correlation.	$+10 \pm .10$	$+ .23 \pm .10$	$+ .16 \pm .10$	$+ .46 \pm .08$	$-.12 \pm .10$

These correlations, however, are low and seem to indicate that the natural varietal traits were being overcome and obscured by other variable factors.

Contrary to expectation, the stand had little to do with the percentage of leaves, as the following low and inconsistent correlations show.

TABLE VII

CORRELATION BETWEEN THE PERCENTAGE OF LEAVES AND STAND			
Cutting	1st	2d	3d
Correlation	$-.14 \pm .10$	$-.02 \pm .10$	$+ .03 \pm .10$
Cutting	4th	5th	6th
Correlation	$+ .10 \pm .10$	$+ .07 \pm .10$	$+ .24 \pm .10$

On the other hand, the relation between height and yield and percentage of leaves was constant and marked, except in the last two cuttings.

TABLE VIII

CORRELATION BETWEEN PERCENTAGE OF LEAVES AND HEIGHT AND YIELD			
Cutting	1st	2d	3d
Yield	$-.41 \pm .08$	$-.60 \pm .07$	$-.15 \pm .10$
Height	$-.48 \pm .08$	$-.62 \pm .06$	$-.68 \pm .05$
Cutting	4th	5th	6th
Yield	$-.40 \pm .09$	$+ .20 \pm .10$	$+ .30 \pm .09$
Height	$-.55 \pm .07$	$+ .09 \pm .10$	$+ .19 \pm .10$

The sudden change from minus to plus in these correlations should be noted. The average heights of the first four cuttings were 32, 30, 28 and 27 inches, respectively. The average height of the fifth and sixth, were 15 and 12 inches. This would suggest that at or below 15 inches the mutual shading of the stems is not sufficient to cause an appreciable shedding of the lower leaves. Up to this point, moreover, growth usually takes place by an increase

in the number of nodes, each with its accompanying leaves and side branches. Above fifteen inches, however, the principal growth in height consists in a lengthening of the internodes and, consequently, a relatively greater production of stem as compared with leaf tissue. In this physiological correlation lies the core of the difficulty in breeding at once for quality and quantity. The act of high production within itself cuts down the quality of the product by reducing the ratio between the leaves and the stems.

This difficulty, moreover, occurs in the composition as well as the percentage of the leaves. The correlation existing between the nitrogen content of the leaves and the number of days required to mature a cutting is shown in the following table:

TABLE IX
CORRELATION BETWEEN THE NITROGEN CONTENT OF HAY AND THE PERIOD
REQUIRED FOR MATURITY

	1st	2d	3d
Cutting Correlation	$-.33 \pm .09$	$-.30 \pm .09$	$-.27 \pm .09$
	4th	5th	6th
Cutting Correlation.	$-.52 \pm .07$	$-.50 \pm .08$	$-.17 \pm .10$

Quickly maturing varieties thus have leaves richer in nitrogen than those which require a greater length of time for completion of growth. When, however, we take the average number of days required throughout the season to mature a cutting for each plot and compare this with the total seasonal yield we find a correlation of $+.43$. Thus we are again confronted by a minus correlation between quality and yield which must be overcome if we would make progress simultaneously in both lines.

As further examples of antagonistic correlations, a few instances may be taken from the data furnished by forty-three plots of pure races of alfalfa grown during the summer of 1910. The correlation between height and percentage of leaves was again constant and marked. The results here paralleled those found for the regional varieties. Whereas yield was uniformly correlated positively with both stooling capacity (av. No. stems per plant) and height, it is interesting to note that there was also a uni-

TABLE X
CORRELATION IN PURE RACES

Correlation Between	Cuttings			
	July	August	September	October
Green weight and average number stems.....	+ .75 ± .04	+ .42 ± .08	+ .62 ± .06	+ .56 ± .08
Green weight and average height.....	+ .01 ± .10	+ .44 ± .08	+ .22 ± .10	+ .33 ± .09
Average height and number of stems.....	— .29 ± .09	— .19 ± .10	— .32 ± .09	— .21 ± .10
Average height and per cent. leaves.....	— .39 ± .09	— .15 ± .10	— .55 ± .07	— .51 ± .08

form minus correlation existing between them. We thus have two factors both making for yield, but seemingly (probably physiologically) antagonistic to each other. In breeding for high yielding strains we are here again called upon to overcome by selection an antagonistic physiological correlation.

This brings us to the following final conclusion which the writer wishes to emphasize:

In economic plant breeding one frequently encounters physiologically negative correlations such as those, in alfalfa, between height and stooling capacity, height and percentage of leaves, and between yield and quality. In seeking improvement, therefore, the breeder must recognize and make use of these facts in the interpretation of results obtained, and also search for races which violate such naturally antagonistic correlations to the greatest possible extent.

GENERAL CONCLUSIONS

That the complex of allelomorphs, which we call a variety, may be definite as both to ultimate composition and organization is not here questioned. When, however, we consider that visible characters are only the expression of the reactions of the vital forces of the plant with the environment, we can realize that the variety, as we see it, is not a definite thing, but is a result of two independent classes of factors. Change either and the result correspondingly changes.

We are therefore to look upon the variety as a delicately organized chemical compound. The various factors of climate and soil may be compared to different physical influences to which the original compound may be subjected. As the chemist would expect reactions varying in accordance with the physical stimuli used, so will the plant react in agreement with the different environmental combinations. The extent to which this will change the nature and appearance of plants is often far reaching. Cook, working with cotton, has found that certain cultural conditions at an early stage of growth will make profound differences in the method of branching which determines the whole subsequent development of the plant and affects materially its economic value. Cultural and climatic reactions often lead to error among those who assume them to be mutative changes induced by the new conditions. That these reactions may bring to light sub-races with hereditary tendencies not hitherto called into expression and which, by selection, may be secured as pure races, is the probable explanation of many cases of supposed direct climatic adaptation.

Thus, realizing the true nature of a variety, we can draw further upon the analogy of the chemist who investigates an unknown substance by testing its reactions with a large number of known reagents. In like manner the breeder can only understand the true nature of the hereditary vital forces within a plant after he has tested and calibrated its reactions against a variety of soil and climatic factors. These reactions are of interest to the farmer only in so far as they affect the economic value of the variety as grown in his own locality but to the breeder and student of heredity their importance is fundamental. This is so because they enable him to classify, coordinate and interpret the experimental results that he obtains. This ability finally must form the basis of all rational procedure, whether one be engaged in the study of pure genetics or in the operations of practical plant improvement.

TAXONOMY AND EVOLUTION

By X.

"Some passages in this book, if taken alone and read hastily, may appear to discourage systematic Zoology. This is far from my intention. No one can study the great naturalists of the seventeenth and eighteenth centuries without feeling how seriously their work is impaired by the defective systems of the time. It is not systematic but aimless work that I deprecate—work that springs from no real curiosity in Nature and attempts to answer no scientific questions."—L. C. Miall, "Natural History of Aquatic Insects," Preface, p. i.

INTRODUCTION

LINNÆUS bestowing Latin names upon animals and plants was simply tripping gaily across the back of a half submerged Behemoth and mistaking it for dry land. Now the beast is careering around, and in spite of zoological congresses and international rules nobody quite knows what to do with him. No doubt when some zoological czar arises and issues his fiat a uniform system of nomenclature will be adopted and things will begin to straighten themselves out. This can only be a matter of time—the past can not be altered. On systematists to-day necessarily devolves the dull, difficult and important duty of going through the descriptive work of the early naturalists and emending it; so that Spallanzani's derisive sobriquet of "nomenclature naturalists" was a little unjust, even in his time.

Whatever opinions may be held upon the genius of Linnæus, in justice to him it should be said that it was not until his example had been followed by a crowd of other workers eager to attain to immortality by way of the back door he had left open that the fat was really in the fire.

Well knowing the confusion into which systematic work in zoology was brought by the early naturalists, modern systematists in our opinion will be the authors of a similar confusion in the future if some of the slipshod methods of modern systematics are not corrected. Moreover, a confused nomenclature is not the least of the evils which second-rate systematic work brings in its train.

Systematists with a proud curl of the lip may tell us that the work is not done now as it once was. Indeed, to those who are not able to project themselves into the future it may seem incredible that the systematists of a later date will be able to find much room for complaint in the elaborate descriptions and careful figures of modern descriptive writers. For the moment, however, it suffices us to point the parable by remarking that in 1780 Spallanzani was able to refer to the "beautiful figures" and "careful descriptions" of a systematic worker on frogs. We, of course, know without seeing them that the figures were not beautiful nor the description, careful—any way in the sense of being complete. We have therefore to reflect whether the zoologists of a future generation will find the work of to-day any freer of faults than that of the past centuries.

SYSTEMATIC WORK. GENERAL CONSIDERATIONS

It is necessary to insist at once that systematic work is not merely a question of nomenclature, names and novelties. Systematists have only themselves to thank if such a narrow conception of their province is very widely spread, especially among morphologists and anatomists, who are ready to belittle the value of the systematists' work. But science is measurement and zoology—if you like—is description, and it is impossible to dispense with the systematists' descriptive work. But we think it possible to dispense with a good deal of stuff after this fashion:

Metopidium high, suprahumeral rather long, acute, arcuate and curved at the tips. Pronotum roughly punctured at the bottom of fine furrows. Color dark-ochreous. Posterior horn uniformly cylindrical, undulating or sinuous without rugosities. Underside, scutellum and legs sordid-ochreous.

The phrase "sordid ochreous" comes ready to hand and makes it unnecessary for us to go in search of a suitable comment.

"This is the 30th memoir" writes a systematist "on the Zonitidae which I have published in this journal, describing in all about 560 new species." We feel inclined to put our hands resolutely on his shoulders and inquire if he ever saw a ctenophor swimming in the sea or watched the progress of an *Asterias* towards its prey.

No one can look unmoved upon the Hymenopteran or Helicoid specialist with head bent over a drawer full of shells or dried insects on pins. It is not that we resent concentration or enthusiasm or even specialization, but the systematist has lost touch with his own science of zoology.

Zoology, a cornucopia of marvels, lies at his elbow full to overflowing, but he is unmindful of it. It is as if a man should use the Parthenon only as a convenient place on which to strike a match for his pipe.

The divorce between systematic work and the rest of zoology is the more regrettable because it is practically complete. It is, we admit, expedient that zoology should be divided up into anatomy, morphology and so on. But such a division is allowable only when it is expedient, while for intellectual purposes such a division is and has always been a danger. To obtain facts one must be an analyst, to consider them one must be a synthesist. Between the two there is all the difference between a hodman and a natural philosopher.

But our contention is that not even the plea of practical expediency can justify the extreme state of specialization into which systematic zoology has fallen, making itself manifest in the concatenation of such purely artificial characters as that "the third joint of the antenna is longer than the second, that the mesoscutellum is ovate and the color pink with blue spots." All this simply makes one yawn, though there is this much to be said in favor of this stamp of systematist, that nothing bores him so much as the recitation of one of his own diagnoses or being introduced to the systematist of another group.

Systematic work is a withered branch of the biological tree which there is still hope of rejuvenating. Treviranus long ago remarked that if we once regarded systematic work as a part of biology and nomenclature as a means to an end rather than as an end in itself, both might take their places in science. Let us take every precaution against systematic work becoming one of those unproductive and artificial pursuits which spring up like mushrooms around centers of splendid endeavor and high achievement. After Shakespeare came his commentators. Shall it be said that after biology came the systematists?

We assume that the principal object of systematic work is to discover the *phylo-genetic classification* of animals, for which it is surely necessary that every animal as it passes through the

systematists' hands should be, as far as possible, thoroughly examined and described, no dependence being placed upon a few superficial characters usually selected from the external parts? That the systematist should concern himself, as he does, with the external parts, leaving the anatomy to other workers, we consider is as bad for the systematist himself as it is bad for the science; for himself, he is doing work which can only keep his soul alive with difficulty—superficial clerical work which can be “prompted by no real curiosity and attempts to answer no scientific questions,” and the results of the work itself is often invalidated by the arrival of the destroying angel in the person of the anatomist. For a superficial description often means a wrong classification; whence it follows that any zoo-geographical deductions therefrom are invalidated; while a careless description usually ignores the possibilities of variation and shows no evidence of pains having been taken to make identification easy.

Systematic work, then, is concerned with classification, geographical distribution, variation and identification, and there would be no need for this paper, if it were more generally realized that one thorough examination and description of the whole animal assists those branches of the inquiry more than twenty loose and superficial ones.

Of course systematic workers are not the only zoologists who over-publish; yet they especially might cultivate a little of the salutary reticence of C. L. Nitsch and Alfred Newton, who, with no discredit to themselves, wrote and published little, yet it must be admitted by those with an eye on the extravagant output of others, to the advantage of zoology. The words “*res non-verba*” were the motto of Delle Chiaje, who, like Nitzsch, on his death left behind many important discoveries unpublished and only indicated in his drawings.

CLASSIFICATION IN GENERAL

The coming of Evolution meant for systematic workers that no system of classification would henceforth be considered as a serious contribution to science, which was not constructed on phylogenetic lines. It meant the final overthrow of such ideas as Agassiz held, that the divisions of the animal kingdom were instituted by the Divine Intelligence as categories of his mode of thought—of such fantastic systems as those of Rafinesque and Swainson and such strictly artificial ones as the arbitrary ar-

rangements of convenience which should be now used only in those groups where, and for as long as, our knowledge of the anatomy is so slight that some sort of temporary device for sorting out genera and species has to be adopted.

The ideal system is now phylogenetic, *i. e.*, it aims at reconstructing in a genealogical tree the actual lines of descent.

Only those who have attempted the reconstruction of phylogenetic trees understand the intrinsic difficulties of the work. There can be no doubt that the coming of Evolution has put before the systematist a very difficult task. As to whether the methods usually employed by him are adequate to the demands placed upon them we are frankly sceptical.

Fortunately for the systematist the main lines of classification in most groups are given him ready made by the morphologists who have laid down the foundations trusting to the "systematist" to fill in the details. Such classifications—the main phyla, classes and orders are of permanent value, because they are founded upon a combination of characters of tried worth judiciously selected after a careful survey of extensive embryological and anatomical data.

SINGLE CHARACTER CLASSIFICATION

On the other hand the minor systems—the families, genera and species—the realm of the "systematist"—too frequently consist of haphazard combination of a few characters selected because of their convenience in not entailing any anatomical work, or selected on account of the ignorance existing of any other—particularly internal—important characters. Ignorance of their morphology has been the main reason for the difficulty in classifying the Coleoptera. Entomologists are especially prone to give their whole attention to what is visible without the aid of dissection. In the Polyzoa the majority of forms are only known by their external appearance and their classification is proportionally unsatisfactory. In the Mollusca reliance is placed on the shell; in mammals the skull and the skin, in birds the plumage are the articles of faith.

Single character classification or diagnosis by one or two characters, as zoological history shows, has proved inadequate—that it is unphilosophical is patent to all.

Such single character classification even when practised by

the great morphologists, men who, being acquainted with the whole of the anatomy of the forms they were classifying, deliberately selected one or two characters after a survey of the whole—was rarely a success. Huxley set out unabashed to classify birds by their palate, and Agassiz fish by their scales—systems which have now shared the fate of most others which set out to erect a classification on the modifications of a single organ alone. Alfred Newton said that there was no part of a bird's organization that by a proper study would not help to settle the great question of its affinities.

The systematist who deals with the minor subdivisions of the animal kingdom—families and genera—should be as much a morphologist as the one who deals with the larger—the phyla and classes.

DESCRIPTION

We have pointed out above that the adequacy of a system of classification depends in great measure upon the thoroughness of the description of the species and genera. Classification in all groups has progressed in just proportion to the more exact examination of the species considered in the classification.

The history of zoological research brings out this fact very clearly, beginning with the work of Linnæus, the originator of the superficial diagnosis, passing on through Cuvier, who appreciated the value of anatomical knowledge, to Von Baer, who emphasized the importance of embryology.

It was not a "systematist" as we know him who first correctly classified *Lepas*—the conchologists blindly accepted it as a Mollusc. It was not a "systematist" who first established *Peripatus* as an Arthropod, for the first describer of that animal regarded it as a slug!

How rare it is to find in a description of a new species anything more than an indication of the external parts. It is a peculiarly arbitrary limit to a man's curiosity that restricts his enquiry to the superficial aspect of an animal. A natural philosopher ought never to be satisfied with the external appearance of things. The wisdom of the ancients bids us "beware of what things appear"; and the method of our modern science is one of close and detailed observations. In scattering names broadcast with liberal largesse upon species, varieties and

genera, systematists have sometimes dropped into some curious errors. Teratological specimens have been described as new species and most zoologists have heard of the man who described as a new species the longicorn beetle, the head of which having fallen off, had been fixed on upside down. His examination of a new species makes so slight an impression on his mind that sometimes the same worker has described the same form twice under different names.

The descriptive papers on Mollusca usually consist of short descriptions of the shells, even written in a dead language. This is conchology. Conchologists confine themselves to the patterns and shapes of shells—nature's medallions—numismatics! Much of this work—along with similar productions in entomology and carcinology—we regard as positively flagitious.

Sir Ray Lankester in the article "Zoology" in the *Encyclopædia Britannica* (ed. XI.) remarks that museum naturalists must give attention to the inside as well as to the outside of animals and that to-day no one considers a study of an animal's form of any value which does not include internal structure, histology and embryology in its scope. Agassiz, too in his famous "Essay on classification" wrote that "the mere indication of a species is a poor addition to our knowledge when compared with such monographs as Lyonnet's *Cossus*, Bojanus' 'Turtle' Strauss Durekheim's *Melolontha* and Owen's *Nautilus*."

"But," it will immediately be asked in chorus, "do you seriously suggest that a monographic volume should be devoted to every new species?"

This is a leading question which brings us to the crux of the whole matter, and can not be answered in simple "Yea" or "Nay."

THE PROVISIONAL DIAGNOSIS

The amount of analytical study that may be given to any one animal form in any one stage of its development is infinite. The result is that in describing a new species for the purposes of exact phylogenetic classification there must be a limit beyond which it is unnecessary to go. Such a limit can not be otherwise than arbitrarily selected according to the best judgment of the systematic worker as to how much analysis is required to place his new species, although at present, *miserabile dictu*, relatively

very few animals have been thoroughly explored, yet in the distant future, in the millennium, it can not be doubted that every genus, even every species will have been examined *in toto* in every stage of its development and life-history as thoroughly as our instruments and eyesight will allow, and perhaps a whole volume or several volumes will be devoted to every animal form. At present, however, it is a waste of ink to consider a future so far away. A more pressing duty is to consider how far modern methods of superficial diagnosis fulfil the obligations placed upon systematists not to give an exhaustive analysis of animal forms, but to give sufficient data to meet the searching demands of phylogenetic classification.

We are aware of the fact that the convinced and determined systematist does not maintain that the method of superficial diagnosis does meet or is intended to meet the demands we have been indicating. If he reads as far as this and does not throw aside this paper in contempt, he is ready with eager forefinger and glib apology to convict us of begging the question that systematic zoology can be ever anything, or should be ever anything more than we have said.

It is often argued that the superficial diagnosis of the systematic worker is simply a provisional diagnosis awaiting the confirmation of the anatomist. A plausible defence of the provisional diagnosis is advanced by many workers in perfect good faith which it is now necessary to anticipate and examine.

This argument defends the provisional diagnosis on two grounds: (1) The advertisement theory; (2) the recognition mark theory.

The supporters of these theories admit that the provisional diagnosis in no way settles either an animal's systematic position or its validity as a species. But it is alleged to be of value and should be encouraged because it advertises the existence of a presumptive new form which would otherwise remain unknown and overlooked in the store rooms of the museum and laboratory, and because in giving an account of the external parts, at all events, the systematist is describing those features by which we are more or less easily able by a superficial examination to recognize summarily the form when it turns up again.

The first part of our answer amounts to a recapitulation of what has been previously stated in general, viz., that systematics have lost touch with the rest of the science. The output of systematic

work and the output of anatomical and morphological work nowadays move along completely different channels. The work turned out by the systematic worker is scarcely, if ever, conceived in the light of modern biological theory, is rarely couched in terms of modern biology and rarely indicates a problem to be solved or a question to be answered. It proposes distinctions the anatomist sweeps away and hazards affinities the morphologist laughs at. It performs work that has to be done over again, and instead of giving the morphologist what it claims to give him—a sketch map of the country he is to traverse—all it does is to bewilder him with a Will-of-the-Wisp's lantern, an intolerable multitude of slipshod and untrustworthy directions that he has come instinctively to suspect. We can not too often ask the question, why should the work be done twice? Surely it is time that something were done to stop this tremendous rush for publishing provisional diagnoses that more time could be devoted to the systematic study of animal forms, obtaining thereby sound phylogenetic classification, sound deductions in geographical distribution, valid species and a less confused nomenclature.

Thus the systematist's protest that at least he "advertises" presumptive new forms we can reply that he may do so, but that for any purpose other than a dull census of the animal kingdom with a very generous "±" to it, he is a positive Benedick of zoologists, for "nobody marks him."

The upholders of the provisional diagnosis will say that at any rate they are giving us a description of the external parts and are increasing our knowledge by so much. True, but by so inconsiderable an amount that when the anatomist comes along with his scalpel he so quickly disposes of the external parts merely by the use of his eyes that it is a matter of indifference whether the former have been described or not. Moreover, the great majority of the tens of thousands of descriptions that are issuing from the press are of animals so closely related to previously described species that such descriptions really amount to little more than a recitation of their distinguishing characters.

It is certainly useful to know that *Caccabis rufa* is to be distinguished from *Perdix cinerea* by its red legs and that the Leporidae can be discriminated by the character of their upper incisors. But the question may well be asked, what is the use of being able to distinguish one species from another without

being able to record at the same time anything about its bionomics or anatomy which would give the distinction its real value. A great deal is known about the partridges and hares, hence the distinctions alluded to above are useful as an easy way of quickly identifying them. But so long as nothing is known about either of two species that are distinguished we are none the worse off, if both remain indistinguishable.

Finally we would point out that of all people the systematist should know that at present of the forms he advertises and describes so copiously and summarily only a fractional part is, or can be, dealt with by the laboratory worker. We are speaking now of the anatomy pure and simple of new species and genera. The laboratory worker proceeds slowly, is fewer in numbers and has other problems—embryology (descriptive and experimental), heredity, physiology (descriptive and experimental) and morphology to attend to besides purely descriptive anatomy. And yet anatomy—the very corner stone of the temple of zoology—has to be restricted in output because none of the systematists will learn how to use a scalpel or look down a dissecting-microscope—feats in themselves perfectly easy and calling for no special training or faculties.

Possibly the upholders of the provisional diagnosis will maintain that by publishing his account of the difference between closely allied forms the systematist is providing the biologist with a stimulus to discover how much deeper such differences go. But surely it is a strange perversion of a man's natural instinct of curiosity that enables the systematist to rest content with advertising problems instead of endeavoring to equip himself for the task of undertaking them himself, who is eminently suited to the work and whose occupation daily brings him into close contact with them.

Finally we would point out that the enormous mass of species which have been created upon superficial diagnosis so far have remained unincorporated for the most part in the structure it is designed to build up, viz., a clear comprehension of the phylogeny of the lesser divisions of the animal kingdom. It is as though a man were to set about building a house by making a vast quantity of bad bricks and then to leave them scattered about his site in the hopes that some one would come along and make a house of them. Surely it is an economy of effort for the systematist to take up the bricks and build himself, what time

the embryologist and morphologist are engaged upon their own special tasks.

THE COMPARATIVE VALUE OF INTERNAL AND EXTERNAL PARTS

Briefly reviewing the discussion as far as we have carried it, it will be seen that we are asking for sound phylogenetic classification of the smaller groups as well as of the larger ones, based not upon single characters, but upon the whole of the characters regarded collectively, for more careful and more thorough morphological methods in description and for the discontinuation of the provisional diagnosis. In view of the desirability of working up sounder schemes of classification from the enormous, unwieldy and superficially known mass of genera and species systematists can be rendering little service by continuing to turn out indiscriminate provisional diagnoses.

It remains now to discuss in greater detail the proposal we bring forward in the place of the provisional diagnosis.

The commonly accepted opinion is that while for the classification of families and orders the internal parts must be taken into consideration, for that of species and genera a summary of the external parts is all that is required. On account of the labor and difficulty sometimes involved in dissection we are too ready to assume that the internal parts in genera and species present a dismal monotony of character which it would be profitless to investigate for systematic purposes.

If it is admitted that internal characters are of value among the higher divisions of the animal kingdom, can the systematist tell us at what precise point in the downward scale they cease to have value, and at which reference need only be made to the external parts? Even supposing for a moment that there is such a limit, we are strongly of opinion that it does not come before the genera.

A genus is of different value in different groups but as a rule it presents so much difference in external form from other genera as to warrant the inference that internal differences of a like extent will be found if sought for. At the present moment a genus is a perfectly arbitrary collection of species. We venture to prophesy that with more elaborate descriptions intergeneric relationships will be more carefully defined and genera will become less heterogeneous and more natural. But this is by the way.

A priori it seems improbable that less variety will be found among the various internal systems of organs than in the integumentary or exoskeletal parts. But an argument may be put forward that the external parts in immediate contact with the environmental forces would be the first to register change in the modification of a species. The internal parts as stanchions and bulwarks remain firm to give characters to orders and families, while change makes assault without and gives characters for species. For example, among the Asteroids it is said that the internal organization is so uniform that the only method of classification is to take the different ways in which the demands of the external environment have been met.

But generally speaking a species depends for its survival not simply upon the external front it presents to its environment. An animal's form cannot arbitrarily be divided into external and internal parts. It is an integral whole, and variation and selection may occur anywhere, while the correlation of variation is a text-book commonplace. As opposed to correlative variation there is the law of the independent variation of parts. Not only may variation occurring in one part cause a variation to take place in another, but variation may take place independently in some areas and be limited in another, so that in deciding upon the comparative value of the internal and external parts in any group consideration must be given to both these laws. In the Asteroids, we assume that anatomists have taken the matter in hand and found that the external parts vary as a rule independently of the internal which remain constant. But in how few groups has such a precaution been taken! Is it not rather the general rule simply to *assume* that the internal parts lack variation and are of no value systematically, as, for instance, in the Lepidoptera, where the Lepidopterists expect that a classification based upon the wing-markings or upon wing-neuration can express the true relationship of the various units?

Even in those groups where systematists have dissected and found the internal parts valueless it still remains necessary, in view of the law of independent and unexpected variation of parts for them, to apply the scalpel to every new form.

It is impossible to deny that the external parts are often of extreme systematic importance—they are exposed to the light and develop color patterns (although color is usually an unsafe guide if taken alone), and the external parts of such forms as

Arthropods and Molluscs being hard provide systematists with a sculpture on which it is easy to detect minute differences in pattern. On the other hand we would remind the conchologist that the external parts are by their very positions most liable to exhibit lesions and weathering, and certainly in the case of Mollusca where the dependence of the exoskeleton upon a specific article of diet (viz., lime salts) is very close, to register "fluctuating variation" according to the constitution of the medium or of the food ingested.

But here again if a more common practise were made in dissecting by systematists, variations would be found even in closely allied species making the descriptions complete and often even necessitating the erection of new genera. One of the writers was dissecting an ordinary species when he discovered that the epipharynx was so entirely different in form and structure from the usual type for the genus that, had it been an external character it would long ago have been formed into a new genus.

Karel Thon¹ has demonstrated how in *Holothyridæ* a single internal structure is at variance with the other indications of genetic affinity. A great many similar instances will be immediately called to mind by those who practise dissection.

Again, if systematists are convinced of the taxonomic value of hard parts how comes it that they need to be reminded that there are hard parts in the internal anatomy as well which they so frequently and habitually leave unnoticed? The endoskeleton of Arthropods, gastric mills, pharyngeal ossicles and cartilaginous supports are all systems which might be profitably studied by the entomologist and carcinologist, while the conchologist generally proceeds as though the radula and jaw were part of the "mush," as he so inelegantly terms the viscera.

GEOGRAPHICAL DISTRIBUTION

The advent of the morphologist into the particular sphere of systematics or the metamorphosis of the systematist into a morphologist (it matters not how we put this desirable event) will result in the annexation not only of classification, but also of questions of geographical distribution by anatomy and morphology. How many pretty theories in geographical distribution

¹ *Zool. Jahrb.*, Bd. XXIII, Syst., pp. 720-21.

have collapsed because they were built on the sands of an incorrect classification? The similarity between the faunas of South America and Madagascar is supported by many facts, but the value of *Solenodon* in Cuba and *Centetes* in Madagascar has been lessened by the recognition that the two genera resemble each other by convergence, and should now be classified in different families.

The Dendrobatinae also are considered by Dr. Gadow as an unnatural group, the two divisions—South American and Mascarene—having, according to him, lost their teeth independently. Again, Dr. Gadow refers to the Ratitae as a heterogeneous assemblage of birds which is “absolutely worthless” for the zoogeographer. There are scores of such artificial groupings—the work of the systematist—which have led zoogeographers astray.

The result is that systematic work as at present pursued is of very little use to us in the study of geographical distribution. It is hopeless nowadays for a zoologist to sit down with a list of species and their range and trusting implicitly in systematic work to make maps of distribution and, as he so often does, to draw deductions therefrom, for the validity of such deductions must ultimately depend upon the anatomical and morphological data. Moreover the study of geographical distribution is developing new methods of tackling its problems.

We do not consider it necessary to touch on the other remedies that might be applied with a view to redeeming zoological taxonomy from its present artificial state and to bringing it into line with the rest of biology.

Such remedies—for instance, testing the validity of species by genetic experiment and the intensive study of variation—have been advocated many times before,² although with little success. We believe, however, that the reforms in descriptive zoology we have advocated above are the more urgent.

² Cf. E. B. Poulton, “Essays on Evolution,” 2. “What is a Species?” and K. Jordan, “Novitates Zoologicae,” 3, 1896.

SHORTER ARTICLES AND DISCUSSION

NABOURS'S GRASSHOPPERS, MULTIPLE ALLELOMORPHISM, LINKAGE AND MISLEADING TERMINOLOGIES IN GENETICS

IN a review of Nabours's breeding experiments with grasshoppers,¹ Mr. Dexter makes a distinction between an interpretation of Nabours's and his own, where I fail to see a difference except in terminology. This is so typical of much recent Mendelian work that I am tempted to call attention to it.

Nabours describes a cross between a female with characters *BI* and a male with characters *CE* and comments on the production of an individual with characters *BEI*. He says, as quoted, that the "female parent gave at least one gamete containing the factors for the patterns of both her parents (*B* and *I*) and that this double character gamete was fertilized by one of the *E* gametes which came from the *CE* male."

Dexter prefers to call the supposed exceptional *BI* gamete of Nabours *BceI*, and the supposed *E* sperm which fertilized it *bcEi*, stating that Nabours's terminology would involve multiple allelomorphism, his own linkage. (Nabours uses, I think, neither expression.) Now what is the difference between the two interpretations? Is it anything but verbal? Is there anything significant in the small letters which Dexter has added to Nabours's formulæ? If so, what is their significance? Do they mean any more than the extra zeros in the expression 1.000 as compared with 1.0?

Dexter proposes an experimental test, that the cross be repeated. "If then *BEI* forms should appear again and in these when mated to other forms the factors *B* and *I* should be found to stay together to the same extent as they before separated, it would show that close linkage, rather than multiple allelomorphism explains this particular instance." How would it show it? If we take Nabours's assumption that *B* and *I* have exceptionally gone into a single gamete and formed with *E* a zygote *BI.E*, would it be counter to his assumption that they should subsequently hang together and that gametes should arise *BI* and *E*, respectively? Would adding a few small letters to the formulæ

¹ AM. NAT., May, 1914.

alter the case, changing it from multiple allelomorphism to linkage? It seems to me that this is one more case in which a fallacious conclusion is reached in consequence of using small letters for *absent* characters in Mendelian formulæ. Professor James Wilson has pointed out others.

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